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A further contribution to the knowledge of the ethology of the genus *Ceramius* Latreille (Hymenoptera: Masaridae) in the southern and western Cape Province of South Africa

by

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ABSTRACT

Accounts of the ethology of *Ceramius cerceriformis* Saussure, *C. jacoti* Richards, *C. rex* Saussure (previously known only from three specimens) and *C. socius* Turner are given with in addition ethological notes on *C. peringueyi* Brauns, *C. clypeatus* Richards, *C. nigripennis* Saussure, *C. braunsi* Turner, *C. beyeri* Brauns, and *C. lichtensteinii* (Klug). The contribution made to the understanding of the species grouping in the genus *Ceramius* Latreille is discussed in particular with respect to the division of one of these species groups.

INTRODUCTION

The present paper is the sixth in a series of publications (Gess, 1965, 1968 and 1973; Gess and Gess, 1980 and 1986) dealing with the systematics and ethology of southern African species of the genus *Ceramius* Latreille. In the two most recent of the above publications accounts were given of some aspects of the ethology of the three species commonly occurring in the eastern Cape Province: *C. capicola* Brauns, *C. linearis* Klug and *C. lichtensteinii* (Klug), and of some of the more westerly occurring species: *C. bicolor* (Thunberg), *C. clypeatus* Richards, *C. nigripennis* Saussure and *C. socius* Turner.

The genus has been divided into eight species groups (Richards, 1962; Gess and Gess, 1986). Gess and Gess (1986) found that the nest data available indicated that nest characters are sufficiently different between groups and similar within a group to make them useful taxonomic characters for use in conjunction with morphological characters in defining these groups.

The present paper contributes further ethological data derived from observations and investigations made in the Oudtshoorn district (7–12.xii.1986), the Clanwilliam district (7–13.x.1987), the Hester Malan Nature Reserve, Springbok (15–21.x.1987) and at Tierberg, in the Prince Albert district (26.xi–5.xii.1987). These data add to the knowledge of three of the groups and give a first account for a fourth group. They also contribute further foraging data indicating preferences within groups for plants of a common family.

DESCRIPTIONS OF THE STUDY AREAS

The Oudtshoorn district

Three sites along the Kammanassie River to the south of Oudtshoorn were sampled for wasps. These sites were: Frischgewaagd Site 1 (33° 40′ 05″S, 22° 14′ 18″E); Frischgewaagd Site 2 (33° 39′ 29″S, 22° 13′ 18″E); and Onverwacht (33° 37′ 35″S, 22° 14′ 18″E).

The area which lies in a rain shadow being immediately inland of the Outeniqua Mountains receives an annual rainfall of 240 mm. Rain may be received throughout the year, however, spring and late summer are the wettest periods. The soils above the flood plain are relatively coarse grained and are of the Cretaceous Enon Formation. Those of the flood plain are light coloured, finer textured and are of diverse provenance having been carried down from further east by the river. The area lies within Acocks' Veld Type 26, False Karroid Broken Veld (Acocks, 1953 and 1975). The area is characterized by dwarf scrub, with a noticeable succulent element, and with taller shrubs mainly along water courses (Fig. 1).

Fig. 1. Onverwacht, Oudtshoorn district, 6.x.1987.

Tierberg, Prince Albert district

The farm Tierberg lies 25 km to the east of Prince Albert just north of the Swartberg and is consequently drier than the Oudtshoorn sites receiving an annual rainfall of only 170 mm.

Rain may be received throughout the year but March is often the wettest month. The Tierberg River which crosses the farm rises to the north east in an area of sandstone and mudstone of the Beaufort Series, and passes over shale and sandstone of the Ecca Series, shale with bands of chert and containing phosphate nodules and tillite with bands of shale of the Dwyka Series, and to the south west a band of shale and quartzite of the Witteberg Series. The soils of the area are therefore varied and those of the flood plain of mixed origin.

The area which lies within Acocks' Veld Type 26, False Karroid Broken Veld (Acocks, 1953 and 1975) is characterized by low-growing dwarf scrub, dominated by Compositae and Mesembryanthemaceae, with taller shrubs mainly along the watercourses and on the koppies (Fig. 2).

Fig. 2. Tierberg, Prince Albert district, 4.xii.1987.

The site (33° 42′S, 22° 16′ 24″E) favoured for nesting by *Ceramius* species is an area of relatively level ground flanking the Tierberg River in the vicinity of perennial pools. The soil in the area is coarse and gritty, semi-non-friable to non-friable with a high enough clay element to make it malleable when mixed with water.

The Clanwilliam district

Clanwilliam lies in the Olifants River Valley with to the east the Cederberg Mountains and to the west a hilly area with beyond it the coastal plain. Apart from the sandy coastal plain the

whole area is classified geologically as Table Mountain Series. The soils are derived from quartzitic sandstone and shale and are therefore a mixture of sand and clay the proportions of each varying from area to area resulting in their being of variable friability.

The Olifants River Valley to the north of, around and some way to the south of Clanwilliam lies in Acocks' Veld Type 31, Succulent Karoo, and further to the south extending almost to Citrusdal in Type 26, Karroid Broken Veld (Acocks, 1953 and 1975). The high lying areas lie in Veld Type 69, Macchia (Fynbos) and the coastal plain in Type 34, Strandveld. Moll *et al.* (1984) re-described the major vegetation categories in and adjacent to the Fynbos Biome. They categorize the area in the immediate vicinity of Clanwilliam a "Mosaic of Dry Mountain Fynbos and Karroid Shrublands" and the high lying areas to the west and east "Mesic Mountain Fynbos", changing to "Dry Mountain Fynbos" further to the west on the fringes of the coastal plain.

The sites at which *Ceramius* species were collected were Klein Alexandershoek (32° 20′ 20″S, 18° 46′E) (see Gess and Gess, 1986: Fig. 4) situated in Mesic Fynbos, a site 5 km west of Clanwilliam on the road to Graafwater situated in dry Mountain Fynbos, a sparsely vegetated slope above the Clanwilliam Dam (32° 11′ 30″S, 18° 53′ 42″E) and Kransvlei (32° 14′ 3″S, 18° 50′ 49″E) (Fig. 3) (see also Gess and Gess, 1986: Fig 20) which lies in a transition area, the vegetation being a mosaic of Succulent Karoo, Karroid Broken Veld and Fynbos.

Fig. 3. Kransvlei, Clanwilliam district, 8.x.1987.

The Hester Malan Nature Reserve, Springbok

The Hester Malan Nature Reserve lies approximately 12 km to the east of Springbok in the Carolusberg, in the region of Namaqualand termed Namaqualand Klipkoppe characterized by rocky hills and Eindoorn Granite domes and receiving an annual rainfall of 100–200 mm. The soils are coarse and sandy, however, where they have not been disturbed they are non-friable. When trampled the structure is readily broken down and the soils become friable. In the river bed and in water run-off channels on the slopes the soil is friable sand.

The chosen study area was 6 km by vehicle track north from the offices of the Department of Nature Conservation in a hilly area drained by the headwaters of the Droëdap River (Fig. 4). At the time of the study, 15–21.x.1987, the river bed was dry except for a series of pools where water from beneath the sand comes to the surface, trickles across rocks and sinks once more beneath the surface.

Fig. 4. Hester Malan Nature Reserve to the east of Springbok in the Carolusberg. 21.x.1987.

The ground on either side of the river rises at a relatively steep gradient, on the west-facing slope continuing at a steep gradient to the rocky hillcrest and on the east-facing slope evening out to a relatively level stretch before reaching the rocky steep slope of the hilltops. The soils of the east-facing slope are more stable than those of the west-facing slope, support a greater variety of plants and are favoured by ground nesting wasps.

The area lies within Acocks' Veld Type 33, Namaqualand Broken Veld (Acocks, 1953 and 1975). The east-facing slope, that favoured for nesting by *Ceramius* spp. is characterized by dwarf shrubs. The dominant plants are Mesembryanthemaceae. Also common are perennial Compositae.

ETHOLOGICAL ACCOUNTS

The ethological accounts are presented in the context of the eight species groups, based on morphological characters, to which the species have been allocated (Richards, 1962; Gess and

Gess, 1986). The species composition of each group and for which species ethological data are available are indicated. Group 2 has been subdivided and the suggestion that it should form two separate groups is discussed.

Group 1.

C. fonscolombei Latreille (Fonscolombe, 1835; Bequaert, 1940 in Richards 1962, foraging record only), *C. caucasicus* Ed. André (Fahringer, 1922 in Richards 1962, foraging record only), *C. bureschi* Atanassov.

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c-h. ?
i. Resedaceae and Plumbaginaceae.

Group 2.

Richards (1962) placed together in this group four species, (*C. cerceriformis* Saussure, *C. schulthessi* Brauns, *C. clypeatus* Richards and *C. peringueyi* Brauns), which to him were both poorly known and taxonomically confused. Gess (1965) removed from *C. peringueyi* the male assigned to that species by Richards and included this male together with a previously undescribed female in *C. richardsi* Gess. The previously unknown female of *C. clypeatus* was described at the same time. In a subsequent paper Gess (1973) sank *C. schulthessi* into synonomy with *C. cerceriformis*. In Gess and Gess (1986) the emended Group 2 was shown to consist of *C. cerceriformis* Saussure, *C. clypeatus* Richards, *C. peringueyi* Brauns and *C. richardsi* Gess. These four species may be separated from the other *Ceramius* species by the following two morphological characters in combination: mid tibia with two spurs and propodeum with spine-like processes or at least very blunt angular projections. The inconsistency of form of the clypeus exhibited by members of the group, however, leads to the view that this group is an unnatural one and consequently it is here split into two as follows: Group 2a consisting of *C. cerceriformis* and *C. peringueyi* which have the clypeus of both sexes unmodified (assumed to be so for the still unknown male of *C. peringueyi); and Group 2b consisting of C. clypeatus* and *C. richardsi* which have the clypeus of both sexes much modified with upturned apical teeth.

Group 2a.

C. cerceriformis Saussure (Gess and Gess, present paper) and *C. peringueyi* Brauns (Gess and Gess, present paper, foraging data only).

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. ?
d. Nest with a relatively long main shaft.
e. First cell terminating the main shaft.
f. Succeeding cells terminating relatively short secondary shafts.
g. Secondary shafts sub-horizontal, grouped to one side of main shaft, not all at same or different depths.

h. A constructed mud-cell within an excavated-cell.
i. Forage plants of the family Mesembryanthemaceae.

Ceramius cerceriformis Saussure

Geographic distribution

Ceramius cerceriformis has been recorded from various sites in the western and southern Cape Province: Calvinia and the Touws River district in the south west; several sites from Bitterfontein northwards to Springbok in Namaqualand; and from Oudtshoorn and Willowmore in the south east (Richards, 1962; Gess 1965, 1968, and 1973). The present observations were made in the Hester Malan Nature Reserve, Springbok where a sample of 16 females and 6 males was taken and at Tierberg, in the Prince Albert district where 10 females were taken.

Plants visited

There are only three records of flower visiting by *C. cerceriformis*. One female was collected on "purple flowers of *Mesembryanthemum* sp. (*sensu lato*) (Aizoaceae)" 10 km South of Garies, 7/8.x.1967 (F. W. Gess and W. H. R. Gess) (Gess, 1968), and a second female was collected on flowers of *Psilocaulon acutisepalum* (Berger) N. E. Br. at Mesklip (29° 48′S, 17° 52′E), 1.x.1985 (F. W. Gess and S. K. Gess). This species is also recorded as visiting the white flowers of *Mesembryanthemum crystallinum* (L.) N. E. Br. (Mesembryanthemaceae) at Willowmore, 31.x.1967 (C. F. Jacot Guillarmod) (Gess, 1973).

Provision

Pollen was obtained from provisioned cells from both sites. The pollen grains from both sites are spherical, thin, smooth walled, 25 μ in diameter and of the "mesem" pollen type.

Water collection

Females of *C. cerceriformis* were observed collecting water from small pools in the river bed and from a puddle in a rut in the road in relatively close proximity to the single nest located in the Hester Malan Nature Reserve. Whilst filling their crops these wasps stood on the very wet soil at a short distance from the water's edge.

Description of the nesting areas

Only two nests of *C. cerceriformis* were located. Nest 1, located in the Hester Malan Nature Reserve, was in a bare area between low growing plants in the gently sloping area between the steeper slope above the river and the rocky hills on the western side of the river, that is facing east. The other, Nest 2, located at Tierberg, Prince Albert district, was between low growing plants in more or less level ground above the steep bank of the river.

Description of the nest

Both nests (Fig. 5) consisted of a multi-cellular subterranean burrow surmounted by a short cylindrical mud turret. The turret walls, which were unusually thin, were constructed from mud pellets cemented together and smoothed on the inside. The burrow consisted of a main shaft which descended sub-vertically and then turned sharply to one side to end in a sub-horizontal cell, one of a group of cells, six cells in Nest 1 and two in Nest 2, all/both lying to the same side of the main shaft and all terminating sub-horizontal secondary shafts. The main shaft of Nest 2 maintained a diameter of 5,5 mm along its entire length, 135 mm, whereas that of Nest 1 though

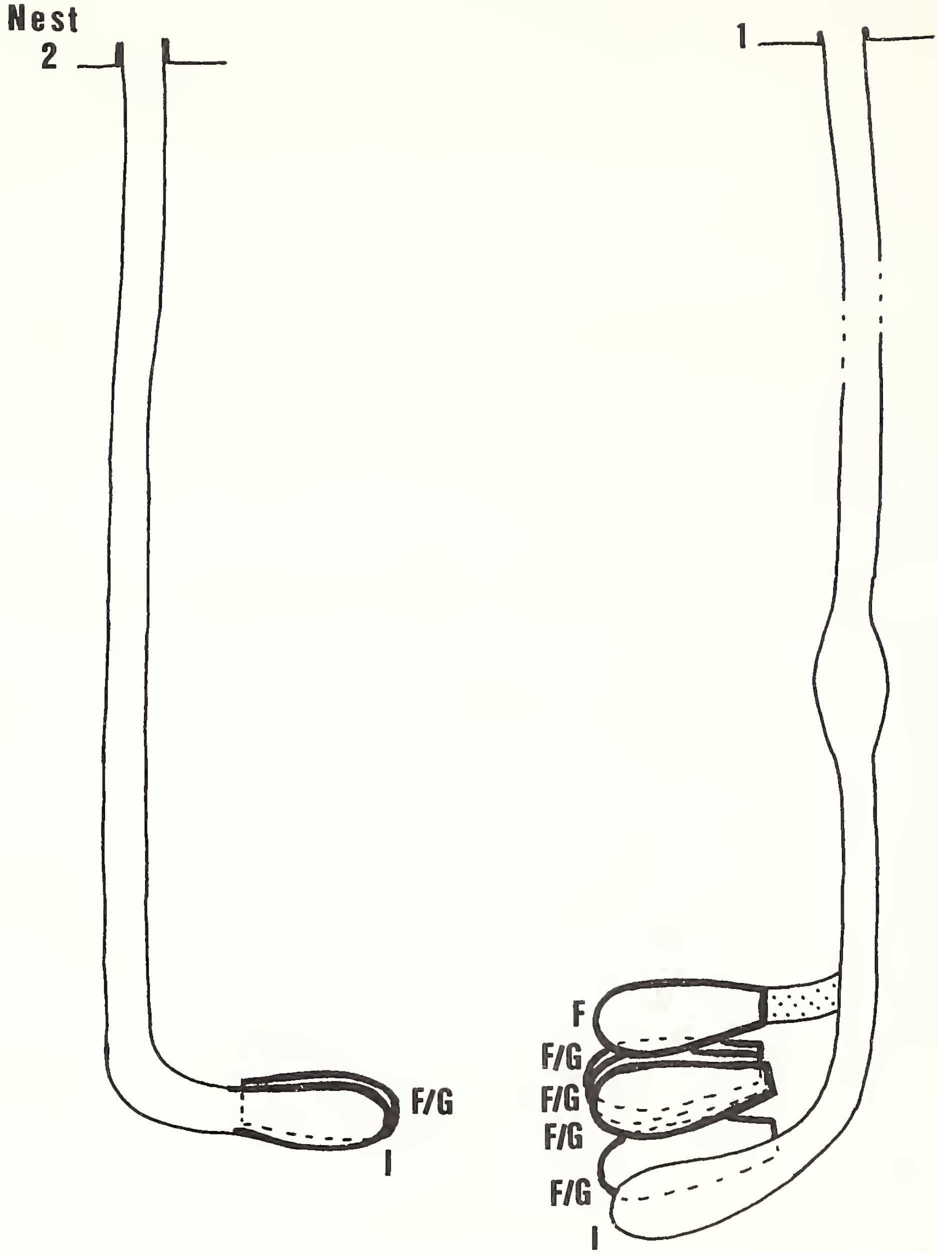

Fig. 5. Vertical plans of turrets and underground workings of nests of *C. cerceriformis* Saussure (× 1). Nest 1, Hester Malan Nature Reserve, 20.x.1987 and Nest 2, Tierberg, 27.xi.1987. For key to lettering see Table 1.

of the same diameter over the greater part of its length was enlarged to form a bulb 10 mm in diameter and 15 mm long at a depth of 95 mm, its total length being 155 mm.

The sealed cells, five in Nest 1 and one in Nest 2 contained constructed mud-cells. The lateral shafts leading to these sealed cells had been filled with compacted earth and their entrances to the main shaft had been sealed off with mud.

The cells were all orientated sub-horizontally and were arranged in two ranks of three ranging in depth from 151–185 mm and all to one side of the main shaft.

The constructed mud-cells were collected. Those from the Hester Malan Reserve are 22, 5 mm long and those from Tierberg are 19 mm long. The diameter at the widest point which is towards the inner end of the cell is 8,5–9 mm in the former and 8 mm in the latter. The walls of all are approximately 1 mm thick, rough on the outside and smoothed on the inside. The completed cells were sealed with a concave mud plate constructed just within the mouth of the cell.

The provision is a firm pollen loaf which is loose in the cell. It is approximately 13 mm long and is 6 mm in diameter over the greater part of its length, however, the first quarter is noticeably narrower being only 2,5 mm in diameter (sample of the five loaves obtained from Nest 1).

Sheltering

The female nest builder at Tierberg was found to be sheltering in her nest at night.

Male behaviour

Males were not observed at flowers or in association with the nest. They were, however, observed at water where they were seen to be pairing with females.

Ceramius peringueyi Brauns

Geographic distribution

Ceramius peringueyi has previously been recorded from Stellenbosch, Het Kruis and Paleisheuvel to the south west of Clanwilliam (Gess, 1965) and is now recorded in addition from a site 5 km east of Vredendal on the road to Vanrhynsdorp.

Plants visited

Fourteen females of *C. peringueyi* were collected foraging on pinkish white flowers of *Psilocaulon acutisepalum* (Berger) N. E. Br. (Mesembryanthemaceae) at the site 5 km east of Vredendal on the road to Vanrhynsdorp situated in Acocks' Veld Type 31, Succulent Karoo.

Group 2b.

C. clypeatus Richards (Gess and Gess, 1986 and present paper, foraging data only) and *C. richardsi* Gess.

a.-h. ?

i. Forage plants, yellow flowered species of Leguminosae.

Ceramius clypeatus Richards

Geographic distribution

Ceramius clypeatus has been recorded from various districts of the western Cape: the Citrusdal district; the Clanwilliam district; and the Het Kruis district to the south west of

Clanwilliam (Richards, 1962; Gess, 1965; Gess and Gess, 1986). The present observations were made in the Clanwilliam district. Fourteen females were collected.

Plants visited

Gess and Gess (1986) recorded the capture of two males foraging on the yellow flowers of *Aspalathus desertorum* Bol. (Leguminosae) at Klein Alexandershoek, Clanwilliam district. This was a surprising record as previously all known forage plants of *Ceramius* spp. in southern Africa were either of the family Mesembryanthemaceae or Compositae. During the period 7-14.x.1987 flowering plants in the Clanwilliam district were sampled for wasp visitors. *C. clypeatus* was found foraging only on *Aspalathus desertorum* from which specimens were taken at the Clanwilliam Dam (14.x.1987, 10 females) and at a site 5 km west of Clanwilliam on the road to Graafwater (12.x.1987, 4 females).

Group 3.

C. nigripennis Saussure (Gess and Gess, 1986 and present paper), *C. toriger* Schulthess (Gess, 1968, foraging record only), *C. braunsi* Turner (Gess and Gess, present paper, foraging record only), *C. jacoti* Richards (Gess and Gess, present paper), and possibly *C. micheneri* Gess.

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest perennial (confirmed for *C. nigripennis* only).
d. Nest with relatively short main shaft.
e. First cell terminating main shaft.
f. Succeeding cells terminating extremely short secondary shafts.
g. Secondary shafts sub-vertical and all of comparable depth.
h. A constructed mud-cell within an excavated-cell.
i. Forage plants of the family Compositae.

Ceramius nigripennis Saussure

Geographic distribution

Ceramius nigripennis seems to be a Namaqualand species, having been recorded from various sites in that region: Swart Doringrivier, between Bitterfontein and Garies; Garies; Kamieskroon; Bowesdorp; Mesklip; and a site 8 miles east of Springbok on the road to Pofadder (Richards, 1962; Gess, 1965 and 1968; Gess and Gess, 1986). During the present study it was found to be extremely abundant in the Hester Malan Nature Reserve, Springbok.

Plants visited

Gess and Gess (1986) recorded *C. nigripennis* provision to contain pollen which matched that of the orange flowered *Dimorphotheca sinuata* DC. (Compositae). In the Hester Malan Nature Reserve a female was observed on the yellow flowers of *Pentzia suffruticosa* (L.) Hutch. ex Merxm.(Compositae) and a male was collected on the yellow flowers of a composite *cf. Berkheya.*

Water collection

In the Hester Malan Nature Reserve females were observed in large numbers collecting water mainly from small pools but also from trickles over rocks and sand in the river bed. Whilst filling their crops these wasps stood on the water (Fig. 6).

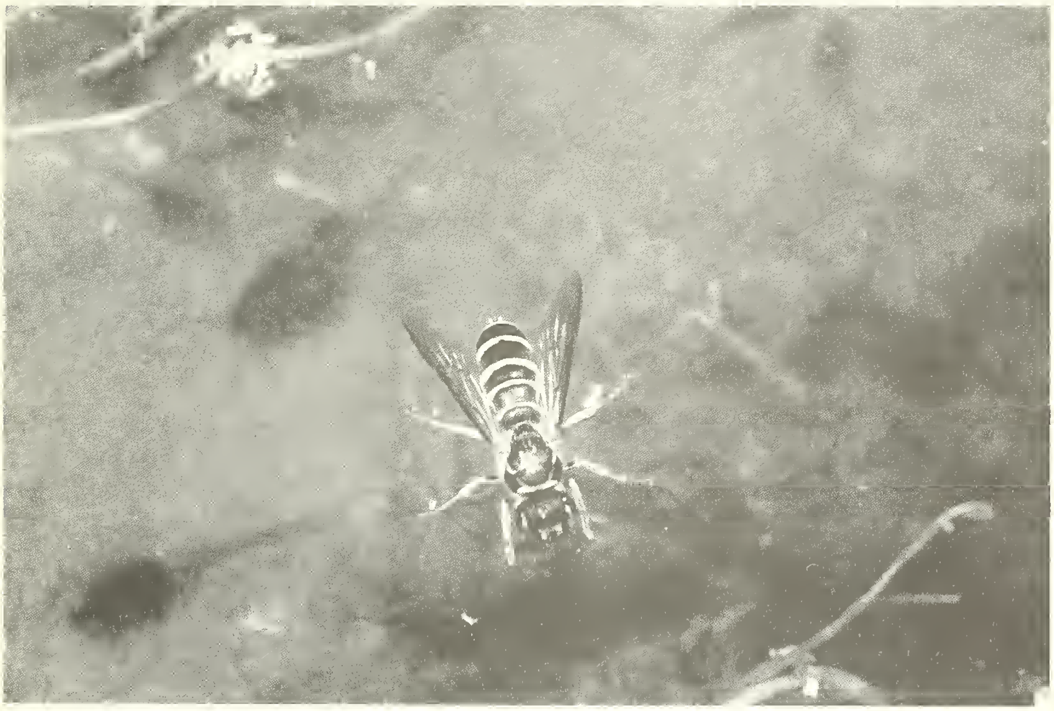

Fig. 6. Female *C. nigripennis* Saussure filling her crop with water whilst standing on the water surface, Hester Malan Nature Reserve, 16.x.1987. Actual length of female 15 mm.

Male behaviour

Male *C. nigripennis* were commonly observed at water in company with the females with which they were seen to pair.

Description of nesting area

Thousands of nests of *C. nigripennis* were located in the Hester Malan Nature Reserve on the west slope above the river, from the river bank to the upper limit of the steeper slope. As at Mesklip (Gess and Gess, 1986) the nests were grouped in relatively small aggregations in close proximity to the bases of bushes on the edge of bare patches. The north sides of bushes seem to be particularly favoured.

Description of the nest, method of construction of the nest, oviposition and provisioning.

See Gess and Gess, 1986.

Ceramius jacoti Richards

Geographic distribution

Ceramius jacoti has been recorded from various sites in the south western Cape: Hex River; Touws River district; Constable; Bloutoring Station; a site 50 km east of Touws River; the Montagu district including Ouberg Pass; Ladismith; and Oudtshoorn in the east (Richards, 1962; Gess, 1965). The present observations were made in the Oudtshoorn district. A sample of 23 females was collected. These additional records are: Frischgewaagd Site 1 , 7.xii.1986, 1 female (H. W. Gess); Frischgewaagd Site 2, 7–8.xii.1986, 5 females (F. W. Gess), 7 females (H. W. Gess), 8 females (R. W. Gess), and 1 female (S. K. Gess); and Onverwacht, 9–12.xii.1986, 1 female (S. K. Gess).

Plants visited

Ceramius jacoti was collected foraging on the yellow flowers of *Pteronia incana* DC. (Compositae), Brandrivier road, 2 miles from the junction with the Ladismith-Riversdale road, 30.ix.1972, by C. F. Jacot Guillarmod (Gess,1973). All those specimens from Frischgewaagd Site 2, listed above, were collected foraging on the yellow flowers of *Senecio rosmarinifolius* L. f. (Compositae).

Provision

Pollen was obtained from a fully fed larva of *C. jacoti* and compared with that of *Senecio rosmarinifolius* with which it was found to be identical.

Water collection

Only one female was observed at water, a puddle in a rut in the road.

Male behaviour

Males were not observed. However, their absence from the nesting area is of interest.

Description of the nesting area

A nesting area of *C. jacoti* was located at Onverwacht. The nesting site was a sloping bank on the edge of a bare area on the vegetated flood plain.

Description of the nest

The nest (Figs 7, 8 and 9) consists of a subterranean burrow surmounted by a curved tubular mud turret roughly smoothed on the outside and well smoothed on the inside with no interstices left open. The turret and shaft opening are of equal diameters. The relatively short main shaft descends sub-vertically. Initially it is of the same diameter as the shaft entrance but after a short distance the diameter increases by approximately 50 per cent and then decreases forming a "bulb" of approximately equal length to the upper part of the burrow. Beneath the bulb the shaft continues for a short distance ending in a cell. The excavated-cell approximates the "bulb" in diameter. Within it is a constructed mud-cell.

As the five nests investigated were new nests and none had reached the stage of cell closure, the description of the nest must perforce for the present remain incomplete.

Method of construction of the nest, oviposition and provisioning

Water is required for nest construction.

Fig. 7. *C. jacoti* Richards, nest turret (× 1,8), Onverwacht, Oudtshoorn, 9.xii.1986.

The turret is constructed at an early stage in nest excavation. At the commencement of turret construction pellets are laid down around the shaft entrance in such a way that the turret will have the same inner diameter as that of the shaft, that is 5 mm (sample of five, no variation). The walls of the turret are approximately 1,5 mm thick. The shaft diameter is maintained constant to a depth of 20–25 mm (average 22 mm, sample of 4) after which the diameter is increased to form a "bulb" 7–9 mm (average 7,7 mm, sample of 4,) in diameter and 20–24 mm (average 21 mm, sample of 4) in length. Beneath the "bulb" the diameter of the shaft returns to 5 mm for a short distance to form a neck to the cell. An excavated-cell of diameter 7–9 mm is prepared and within this a mud-cell is constructed with its walls approximately 1 mm thick and the inner surface of the walls well smoothed.

Only five nests were located. These were excavated and found to be new nests, four of which contained one cell each. No egg or pollen loaf was obtained. One cell contained a large fully fed larva from which pollen was extracted and identified (see *Provision*).

Sheltering

A female *C. jacoti* was found sheltering in one of the nests.

Associated insects

One of the nests was found to have been invaded by a megachilid bee which had constructed a leaf cell within the nest.

Fourteen *Allocoelia capensis* (Smith) (Chrysididae) were collected from flowers of *Senecio rosmarinifolius* where they were found in company with foraging *C. jacoti*. *A. capensis* has previously been recorded as a parasite of *C. lichtensteinii* (Brauns, 1910) and in association with this wasp in its nesting areas (Gess and Gess, 1980).

Fig. 8. Excavation showing burrow of *C. jacoti* Richards cut through vertically, constructed-cell intact, (× 1,8), Onverwacht, Oudtshoorn, 9.xii.1986.

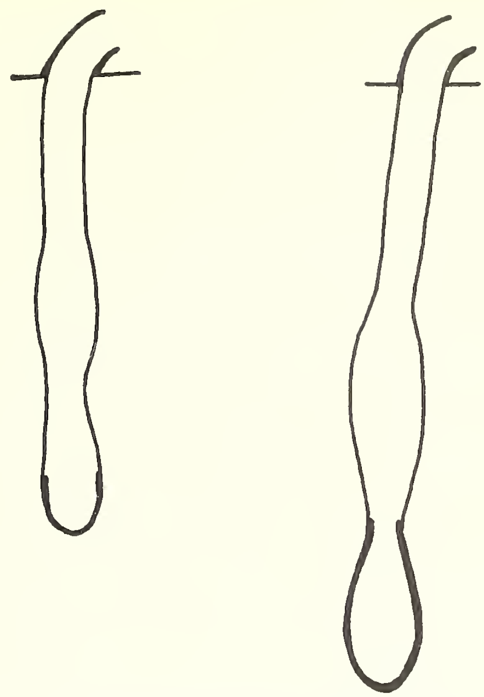

Fig. 9. Vertical plans of turrets and underground workings of two nests of *C. jacoti* Richards (× 1). Onverwacht, Oudtshoorn, 9.xii.1986.

Ceramius braunsi Turner

Geographic distribution

Ceramius braunsi has been recorded from: Olifants River, between Citrusdal and Clanwilliam; Pakhuis Pass to the east of Clanwilliam; Vanrhynsdorp to the north; Worcester to the south east; and Willowmore, the most easterly record (Richards, 1962; Gess, 1965, 1968 and 1973). The present observations concerning this species were made at Kransvlei in the Clanwilliam district during the period 7–13.x.1987. A sample of ten females was collected.

Plants visited

Two females of *C. braunsi* were collected foraging on the yellow flowers of *Athanasia trifurcata* (L.) L. (Compositae) growing at Kransvlei, Clanwilliam district.

Water collection

Six females of *C. braunsi* were collected on very wet sand, that is supersaturated sand covered with a film of water, at the edge of the dam at Kransvlei, Clanwilliam district.

Group 4.

C. beyeri Brauns (Brauns, 1910; Gess, 1973, forage record only; Gess and Gess, present paper) and probably *C. damarinus* Turner

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c-h. ?
i. Forage plants of the family Mesembryanthemaceae.

Ceramius beyeri Brauns

Geographic distribution

Ceramius beyeri Brauns has previously been recorded from: Calvinia; Blaukrans near Calvinia; Cape Town, Beaufort West (*sic*); Willowmore; Cradock; Somerset East; and Grahamstown (Richards, 1962; Gess, 1973). The present observations were made at Tierberg, Prince Albert district, where three females and one male were collected (F. W. , S. K. and R. W. Gess, 26.xi.1987–5.xii.1987).

Plants visited

Gess (1973) recorded a female *C. beyeri* visiting the "whitish flowers" of "mesems" (Mesembryanthemaceae) at the Bible Monument, Grahamstown. During the present investigation one female was collected visiting the white, flushed with pink, flowers of *Sphalmanthus cf. bijliae* (N. E. Br.) L. Bol. (Mesembryanthemaceae).

Description of nesting area

The nesting site of *C. beyeri* at Tierberg was at the base of a stone in a bare area of level ground in dwarf scrub on the left bank of the Tierberg River in close proximity to water.

Description of the nest

A single nest of *C. beyeri* was located. It consisted of a burrow surmounted by a short cylindrical mud turret constructed from pellets cemented together and smoothed on the inside so that no interstices remained. The inner diameter of the turret was equal to that of the shaft, that is 5 mm, and its height was 7 mm. The shaft descended vertically for 20 mm. Unfortunately as no further nests were located the nest plan and the nature of the cells remain unknown.

Group 5.

C. lichtensteinii (Klug) (Brauns, 1910; Gess and Gess, 1980)

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest perennial.
d. Nest with relatively long main shaft.
e. No cell terminating the main shaft.
f. Cells terminating extremely short secondary shafts.
g. Secondary shafts sub-horizontal and each successive cell deeper.
h. A constructed mud-cell within an excavated-cell.
i. Forage plants, shrublets of the family Mesembryanthemaceae.

Ceramius lichtensteinii (Klug)

Geographic distribution

Ceramius lichtensteinii is, for *Ceramius*, a widespread species having been recorded from the Tankwa Karoo in the west to Grahamstown in the east and from the Eastern Cape Province north to Kroonstad in the Orange Free State (Richards, 1962; Gess, 1965, 1968 and 1973).

Description of the nesting area

Gess and Gess (1980) recorded that *C. lichtensteinii* at Hilton and Clifton, both Eastern Cape, show a preference for nesting on raised ground despite the abundance of apparently suitable bare areas of horizontal ground which are favoured for nesting by *C. capicola* and *C. linearis*. It seems of interest therefore to note that at Tierberg, Prince Albert district, where pseudo-colonies of this wasp were extremely common at the time of the authors' visit in December 1987, horizontal ground and raised sloping ground were equally favoured.

Plants visited

In the Grahamstown district, Eastern Cape Province males and females of *C. lichtensteinii* have been recorded visiting flowers of several species of Mesembryanthemaceae (Gess, 1973 and Gess and Gess, 1980). At Tierberg both males and females of these wasps were commonly seen on the white, flushed with pink, flowers of *Sphalmanthus cf. bijliae* (N. E. Br.) L. Bol. (Mesembryanthemaceae).

Description of the nest

The nesting of *C. lichtensteinii*, *C. capicola* and *C. linearis* at Hilton has been described in detail (Gess and Gess, 1980). The diameter of the main shaft of the nests was stated to be related to the size of the wasps. The average diameter of the main shaft of the nests of *C. lichtensteinii* at Hilton was 6,2 mm. It is of interest that the average diameter of the main shaft of the nests of this species at Tierberg was 8,0 mm (sample of 22). This significantly greater diameter can be related to the significantly larger size of individuals of this species at the Tierberg Site. The width of heads measured across the eyes is 5,03 mm (average of 30, range 5,0–5,5 mm) for females from Hilton as compared with 6,35 mm (average of 30, range 6,0–7,0 mm) for females from Tierberg. In other words the diameter of the shafts of the nests at Tierberg is 29 per cent greater than that of nests at Hilton and the width of the heads of the wasps is 26 per cent greater.

Group 6.

C. caffer Saussure, *C. metanotalis* Richards, *C. rex* Saussure (Gess and Gess, present paper)

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest perennial.
d. Nest with a relatively short main shaft.
e. First cell terminates the main shaft.
f. Succeeding cells terminate secondary shafts.
g. Secondary shafts sub-horizontal, in a group to one side, neither all at the same depth nor all at different depths.
h. A constructed mud-cell within an excavated-cell.
i. Forage plant, the yellow flowered *Berkheya spinosissima* (Thunb.) Willd. (Compositae).

Ceramius rex Saussure

Geographic distribution

Ceramius rex is very rare in collections, apparently being known from only three specimens prior to the present study. The type specimen, a female, was described from the Cape Colony by de Saussure in 1855. Richards (1962) without explanation and without having seen the type specimen sank *C. rex* into synonymy with *C. lichtensteinii* (Klug). The second specimen, a female, also not seen by Richards, was collected at Garies in Namaqualand in 1931 (S. A. M. Staff). This specimen was stated by Turner (1935) and Gess (1965), who supported his view with a detailed description of this specimen, to correspond to the description of *C. rex* Saussure. In an unsuccessful attempt to obtain further specimens, Gess (F. W.) collected at Garies during early October 1966 and again at the same time in 1967. The third specimen collected by chance by Dr and Mrs H. Townes at Garies (25.ix.1970) was the long unknown male of *C. rex*. A description of this male was given by Gess (1973).

The search for the elusive *C. rex* was taken up again in September/October 1985 by Gess and Gess (the present authors) and was finally brought to a successful conclusion in October 1987 when it was discovered nesting not uncommonly at a site in the Hester Malan Nature Reserve, Springbok, 100 km due north of Garies. A sample of 39 specimens, 28 females and 11 males, was taken during the period 15–21.x.1987, 12 nests were investigated, a forage plant was identified and both males and females were taken at water.

From the scanty distribution data available it seems likely that *C. rex* is of rather restricted occurrence and may probably be termed a Namaqualand species.

Plants visited

During the period 15–21.x.1987 a wide range of plants in flower in the Hester Malan Nature Reserve was sampled for wasp visitors. Only one instance of plant visiting by *C. rex* was recorded, a female, foraging on the yellow flower capitulae of *Berkheya spinosissima* (Thunb.) Willd. (Compositae).

Provision

Provision was obtained from the cells of *C. rex* from three nests. Pollen grains from the provision and from flowers of *Berkheya spinosissima* were compared. It was found that the provision contained pollen grains identical in size and structure to those from *B. spinosissima* flowers and also grains of apparently the same structure but of a noticeably smaller size (ratio 9:13).

Water collection

Females were observed collecting water from small pools in the river bed. Whilst filling her crop a wasp stands on the water surface.

Male behaviour

Males were not seen on flowers nor in the nesting area, however, they were collected at water where they were observed pairing with the females. It seems that they wait for the females at and around their water collecting source.

Description of the nesting area

A nesting site of *C. rex* was located in the Hester Malan Nature Reserve. The area favoured for nesting by these wasps is gently sloping and lies between the steeper slope above the river and the rocky hills on the western side of the river, that is facing east. The nests occurred in bare areas either singly or more commonly grouped. The nests in the groups were old, old re-used and new suggesting that a newly emerged female tends to nest either in the nest of her origin or else in a new nest excavated by herself in close proximity to the one from which she emerged.

Description of the nest

The nest (Fig. 10) of *C. rex* consists of a multi-cellular burrow surmounted by a curved tubular mud turret. The turret is constructed of mud pellets roughly smoothed on the outside and well smoothed on the inside. Some interstices are left open. The turret and shaft opening are of equal diameters. The main shaft descends sub-vertically and is initially of the same diameter as the entrance but widens after some distance. The wider section of the main shaft varies in length from nest to nest. In some nests it is no more than a turning "bulb" below which the shaft continues downwards with a diameter equalling that of the upper section of the shaft. In others the entire lower section of the sub-vertical shaft is wide. In some nests the diameter of this lower wide section of the shaft fluctuates so that its sides are very uneven. The shaft at the base of its sub-vertical section curves outwards to terminate in a cell which lies sub-horizontally. Sub-horizontal secondary shafts each terminating in a cell fan out from the main shaft but never form a complete whorl so that the cells lie together in a group. In some instances the cells are at different depths and the shafts leading to them leave the main shaft at different depths but always forming a group. Within an excavated-cell there is a constructed mud-cell sealed at the neck with a mud-plate. The section of the secondary shaft between the cell and the main shaft is filled with soil and sealed off from the main shaft.

Method of construction of the nest, oviposition and provisioning

At the commencement of nesting a female may either initiate a new nest or enlarge the nest from which she emerged. Water is required for nest construction. At an early stage in nesting both nest initiators and nest enlargers construct a turret surmounting the excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same inner diameter as the shaft, that is 5,5–7 mm (average 6,7 mm, sample of 10). The walls of the turret are approximately 1 mm thick, the external diameter of the turret being 8–9 mm (average 8,8 mm, sample of 11). Pellets are added to the turret in such a way that the turret soon curves over, the top of the curve being 11–15 mm (average 13 mm, sample of 11) in height. In the construction of new nests, after turret construction has been completed, further pellets extracted in shaft sinking are discarded in a pellet dropping area 100–200 mm from the nest.

In the excavation of a new nest the initial diameter of the shaft is maintained to a depth of 35–84 mm (average 47 mm, sample of 12) after which the diameter is increased to 10–15 mm (average 11,5mm, sample of 10). This diameter is maintained to a variable depth. In some instances the expanded portion is no more than a " bulb" beneath which the shaft returns to its initial diameter. In others the increased diameter is maintained for several centimetres before there is a return to the initial diameter and in still others the shaft continues at an increased diameter for the remainder of its length. Having reached a depth of 85–115 mm (average 103, sample of 12) there is a change in the direction of the excavation of the shaft which curves

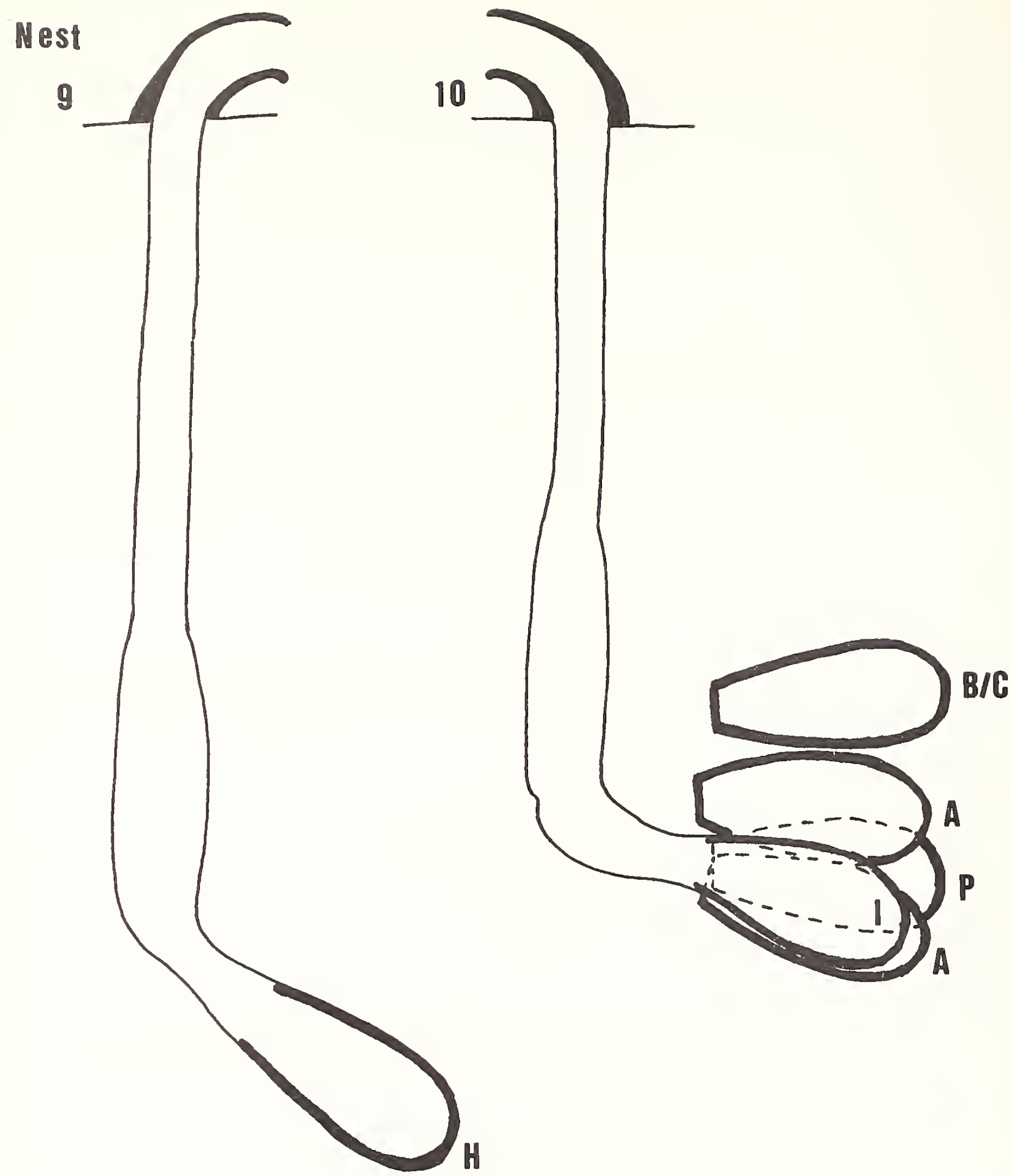

Fig. 10. Vertical plans of turrets and underground workings of *C. rex* Saussure (× 1). Hester Malan Nature Reserve, 20-21.x.1987. For key to lettering see Table 1.

outwards and has a diameter approximating that of the upper section. After a short distance the diameter is increased to 14–17 mm and the excavation terminates in a round ended ovoid cell about 32 mm in length. Within this cell a mud-cell is constructed having a wall 2,5–3 mm thick and being carefully smoothed on the inside.

If a female is nesting in the maternal nest, she cleans out the shaft, constructs a turret, and prepares for re-use the cell from which she herself emerged by cleaning the inside of her cocoon which is left in position.

A new cell having been constructed or an old cell prepared for re-use oviposition takes place. The egg is large , yellow and curved, 6,5 mm from tip to tip across the bow and is laid loosely at the inner end of the cell.

Oviposition having been performed provisioning takes place. The provision, a mixture of pollen and nectar, is a relatively dry and firm loaf of even diameter along its length.

The cell is sealed with a mud plate and the sub-horizontal shaft is then firmly packed with soil until the sub-vertical shaft is reached, when it is sealed off with a mud plate.

Further cells terminate secondary shafts and are prepared in a similar fashion to the first cell of a newly constructed nest. In a re-used nest only the cell from which the possessor of the nest herself emerged is re-used, all other cells and the secondary shafts leading to them are freshly excavated.

A sample of twelve nests was investigated (Table 1). Four were new nests. In all of these

TABLE 1

Details pertaining to 12 nests of *Ceramius rex* Saussure investigated in the Hester Malan Nature Reserve, Springbok on 20–21.x.1987.

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cell contents	Wasp in nest
1	Old, reused	Present	8	A A A B/C B/C B/C F P	female
2	Old, reused	Present	5	A A A B/C F I	female
3	Old, reused	Present	4	B/C B/C F I	female
4	New nest	Present	2	E I	female
5	New nest	Present	2	E I	female
6	Old, reused	Rudimentary	6	A A A A B/C I	none
7	New nest	Present	1	I	none
8	Old, reused	Present	5	B/C B/C F I P	female
9	New nest	Present	1	H	female
10	Old, reused	Present	5	A A B/C I P	female
11	Old, reused	Present	4	A A E H	female
12	Old, reused	Present	5	A B/C B/C B/C E	female

Key: A. Cell open containing old cocoon from which adult wasp has emerged.
B. Cell closed, containing pupa in cocoon.
C. Cell closed, containing pre-pupa in cocoon.
E. Cell closed, containing mature larva prior to cocoon spinning.
F. Cell either open or closed, containing still feeding immature larva.
H. Cell open, containing egg without provision.
I. Cell open, empty.
P. Parasitized.

there was an open cell and in two a closed cell in addition. Eight nests were re-used of which two possessed 4 cells, four 5 cells, one 6 cells and one 8 cells. In nests 1, 2, 8, 11 and possibly 12 more than one of the cells had been re-used (previously re-used cells contain two cocoons, one within the other). As it appears that only one female works a nest, other emergees leaving to start new nests, this would indicate that these nests had been re-used more than once and were therefore probably in their third year of use.

The cocoon is firmly attached to the cell walls except at the outer end which is capped with meconium, this end is separated from the cell closure by a space about 3 mm long.

Associated insects

Three of the nests investigated each contained a cocoon with a small opening in the meconium plug suggesting the emergence of parasites (Table 1). It was not possible to establish what these might have been.

Group 7.

C. hispanicus Dusmet, *C. moroccanus* (G. Soika), *C. spiricornis* Saussure, *C. beaumonti* (G. Soika), *C. lusitanicus* Klug (Richards, 1963, foraging record only), *C. vechti* Richards (Richards, 1963, foraging record only), *C. bischoffi* Richards (Richards, 1963) and *C. tuberculifer* Saussure (Giraud, 1871 and Ferton, 1901)

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c-g. ?
h. A constructed mud-cell within an excavated-cell.
i. Leguminosae, Umbelliferae and Labiatae.

Group 8.

C. bicolor (Thunberg) (Gess and Gess, 1986), *C. socius* Turner (Gess and Gess, 1986 and present paper), *C. linearis* Klug and *C. capicola* Brauns (Gess and Gess, 1980)

a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest annual.
d. Nest with a relatively long main shaft.
e. First cell terminating the main shaft.
f. Succeeding cells terminating relatively long secondary shafts.
g. Secondary shafts sloping.
h. NO constructed mud-cell within an excavated-cell.
i. Forage plants, creeping and shrubby species of Mesembryanthemaceae.

Ceramius socius Turner

Geographic distribution

Ceramius socius is a western Cape species having been recorded from: the Clanwilliam district; Worcester; the Touws River district; Constable; Matjesfontein; Robertson; Montagu; a site 45 km east of Montagu; and Swellendam (Richards 1962; Gess, 1965 and 1968; Gess and Gess, 1986). The present observations were made at Kransvlei in the Clanwilliam district.

Fig. 11. Favoured water collecting point of *C. socius* Turner, wet sand near edge of dam, Kransvlei, 7-14.x.1987.

Fig. 12. Aggregation of *C. socius* Turner at watering point, Kransvlei, 7-14.x.1987. Actual length of females 13,5 mm.

Flowers visited

Gess and Gess (1986) recorded *Ceramius socius* males and females visiting *Psilocaulon acutisepalum* (Berger) N. E. Br. (Mesembryanthemaceae) at Kransvlei in the Clanwilliam district. During the period 7–14.x.1987 plants in flower at various sites in the Clanwilliam district were sampled for wasp visitors. *C. socius* was again found to be foraging only on flowers of *Psilocaulon acutisepalum* and this only at Kransvlei in the vicinity of the nesting site.

Provision

Provision was obtained from 10 cells of *C. socius*. In all instances it was in the form of a firm "pollen loaf" approximately 7 mm long and 4 mm in diameter. Pollen from the provision was compared with that of *Psilocaulon acutisepalum* and found to be identical.

Water collection

Large numbers of females were observed to aggregate at one favoured spot on wet sand near the edge of the dam at Kransvlei (Figs 11 and 12). The same spot and no other was patronized during the period of seven days during which observations were made. The sand became quite pitted from the wasps' activities. Water for crop filling was extracted from the wet sand.

Description of the nesting area

The nesting areas recorded by Gess and Gess (1986) were revisited by the authors in early October 1987. There was no sign of the activity of *C. socius* on the Pakhuis Pass probably due to the lack of water. The nesting site previously in use at Kransvlei had been abandoned in favour of an extensive bare area on the opposite side of the road. This bare area had been created during the construction of a dam and a farm road. The nests were in close proximity to each other and extended over an area of approximately 50 paces by 3 paces. The nearest distance between the dam and the nesting area was 35 paces.

Male behaviour

During the period 7–14.x.1987 males of *C. socius* were common at Kransvlei both in the nesting area and at the dam where the females were aggregating on the mud at a point some little distance from the water's edge. In the mornings the males were the first to appear in the nesting area where they waited for the females which, about an hour later, appeared from their nestswhere they had spent the night. Shortly after they emerge in the mornings the females aggregate, a hundred or more at a time, at their selected point on the mud. The males join them at this "swarming" point and there coupling takes place (Fig. 13). A male having gained a firm hold on a female the pair flies off together. No interactions were observed between males and females either in the nesting area or at the flowers on which, as mentioned, both sexes forage. On a fine day swarming continues until the late afternoon.

Description of the nest

Gess and Gess (1986) were unable to make a full description of the nest as the only nests located by them at the time though turreted had not yet reached the stage of cell excavation. A full description is now possible.

The nest (Fig. 14) consists of a multi-cellular burrow surmounted by a curved tubular mud turret, slightly flared above at the opening. The turret is constructed of mud pellets, rough on

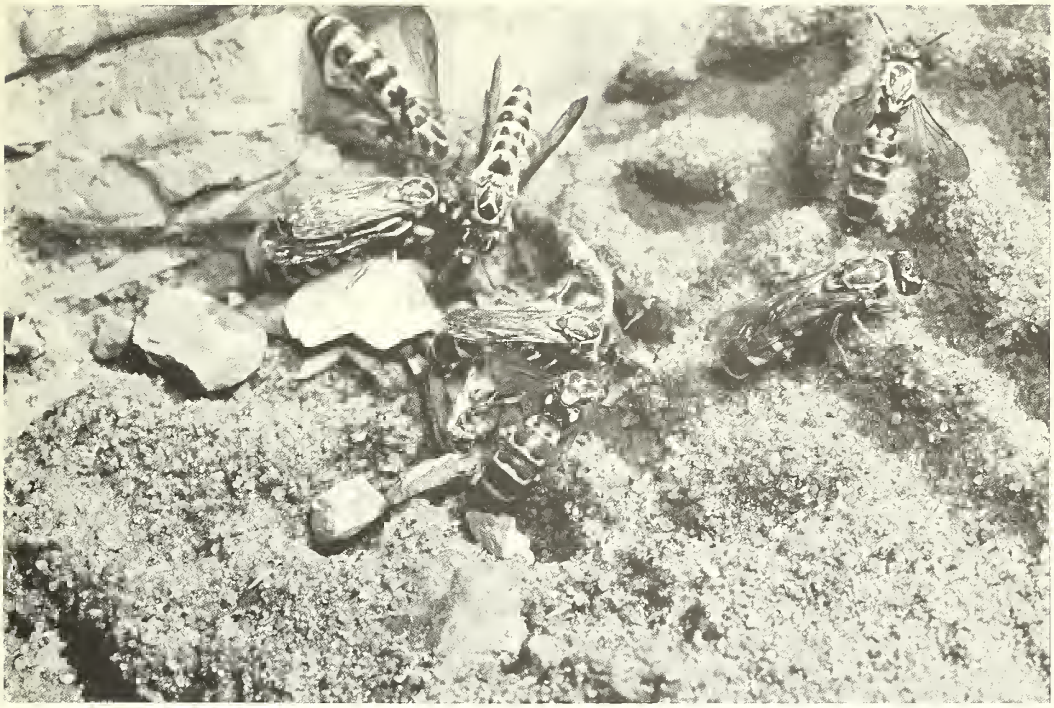

Fig. 13. Coupling male and female *C. socius* Turner at watering point, Kransvlei, 7-14.x.1987. Actual length of females 13,5 mm.

the outside and smoothed on the inside. The turret and shaft opening are of equal diameters. The main shaft, of the same diameter as the entrance, descends sub-vertically before curving to one side to end in a downward sloping to sub-horizontal cell. The main shaft is dilated for a short distance at approximately half its depth to form a "bulb". Secondary shafts diverge from the main shaft at the level at which it departs from the sub-vertical. Each secondary shaft ends in an excavated cell. Secondary shafts between the completed cell and the main shaft are filled withsoil nd sealed off from the main shaft. Mud-cells are not constructed.

Method of construction of the nest, oviposition and provisioning.

No evidence was found of re-use of nests. A female at the outset of nesting initiates a newnest. For this she requires water. At an early stage in shaft excavation turret construction commences. Pellets are laid down around the shaft opening in such a way that the turret will have the same inner diameter as that of the shaft, that is 4,5–5 mm (average of 4,5 mm, sample of 7). The external diameter of the turret is 6,5–8 mm (average 7,2 mm, sample of 8) and the height to which it rises before curving over and downwards is 8–11,5 mm (average 8 mm, sample of 8). After turret construction has been completed further pellets extracted from the excavation are discarded in a pellet dropping area at a short distance from the nest.

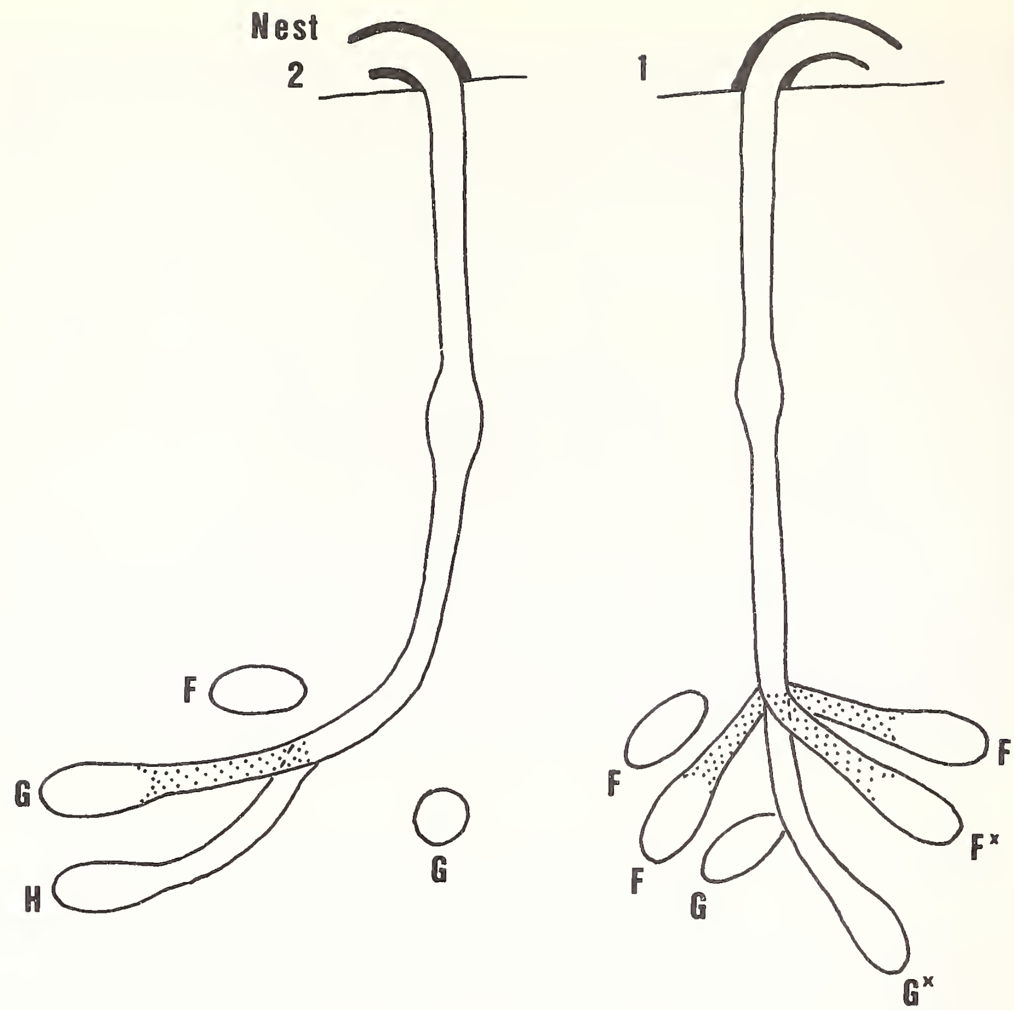

Fig. 14. Vertical plans of turrets and underground workings of *C. socius* Turner (× 1). Kransvlei, 7-14.x.1987. For key to lettering see Table 2.

In the sample of seven nests investigated shaft sinking had been continued downwards with the diameter maintained at 4,5 mm for 17–44 mm after which it had been increased to 6–7,5 mm and reduced again to 4,5 mm in such a way that a short "bulb" 10–13 mm long had been created. Beneath the bulb the shaft had been continued downwards sub-vertically for 29–46 mm.

Below this depth the shaft curves away from the vertical, slopes gently downwards and ends in an ovoid excavated-cell 11–14 mm (average 12,8 mm, sample of 9) in diameter at mid-length. The walls of the cell are carefully smoothed and stabilised. No mud-cell is constructed within the excavated-cell.

After a cell has been excavated oviposition takes place. The egg which is laid loosely in the cell is white, curved and 4–4,5 mm (average 4,1 mm, sample of 5) from tip to tip.

After oviposition has taken place provisioning commences. Successive loads of pollen and nectar are collected in the crop, regurgitated and formed into a firm pollen loaf approximately 7 mm long and 4 mm in diameter.

After provisioning has been completed the sloping shaft between the cell and the vertical shaft is filled with soil and sealed off.

Secondary shafts each terminating in a cell are prepared in a similar fashion. All the secondary shafts leave the main shaft at approximately the same depth, however, they radiate out in different directions so that the cells form a whorl rather than a group.

Seven nests were investigated (Table 2). Two had not yet reached the stage of cell excavation, two were one-celled, two four-celled and the seventh six-celled.

TABLE 2

Details pertaining to seven nests of *Ceramius socius Turner* investigated at Kransvlei, Clanwilliam district, from 7–14.x.1987.

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cells contents
1	New nest	Present	6	F F* G* F H F
2	New nest	Present	4	G H F G
3	New nest	Present	1	I
4	New nest	Present	—	—
5	New nest	Present	—	—
6	New nest	Present	1	I
7	New nest	Present	4	D F H D

Key: * neither egg nor larva found.
D. Cell closed, containing mature larva spinning cocoon.
F. Cell either open or closed, containing still feeding immature larva.
G. Cell either open or closed, containing egg with provision.
H. Cell open, containing egg without provision.
I. Cell open, empty.

DISCUSSION

A fresh consideration of the ethology of the genus *Ceramius* as a whole seems appropriate.

The chosen nesting substrate for representatives of all species groups with the exception of Group 2b is now known and is without exception non-friable to relatively non-friable soil, in all instances with a high enough clay content to make it malleable when mixed with water. The choice of nesting substrate by *Ceramius* seems to be that favoured by most ground nesting masarids for which it has been established, *Jugurtia confusa* Richards (Gess and Gess, 1980), *Masarina familiaris* Richards (Gess and Gess, 1988a), and *Paragia tricolor* Smith (Houston, 1984). The only species known to nest in friable soil is *Quartinioides* sp. which was found in 1985 nesting in friable beach sand at McDougal Bay, Port Nolloth, Namaqualand (Gess and Gess, unpublished field notes).

Ceramius appears to show a preference for horizontally presented soil though some species, *C. lichtensteinii* and *C. jacoti*, will nest in sloping ground, though in the case of the latter the nests were on horizontal "ledges" on the sloping bank. *Ceramius* species have never been found nesting in vertically presented soil, in marked contrast to *M. familiaris* which has been found nesting only in vertically presented soil. The known choice of other species of ground nesting masarids seems to be similar to that of *Ceramius*. *J. confusa* has been recorded nesting in horizontally presented ground and *P. tricolor* in gently sloping ground.

The construction of a mud turret surmounting the burrow entrance is common to all species of masarids nesting in non-friable soil for which nesting is known. All of these species construct cylindrical turrets of the same diameter as that of the shaft. In the turrets of *Ceramius* there is some variation in the degree of curvature and in the degree to which the interstices between pellets are closed. There are, however, no striking differences in architecture between species such as have been described for *Dichragenia* (Pompilidae) (Gess and Gess, 1976), *Bembecinus* (Sphecidae) (Gess and Gess, 1975) and *Parachilus* (Eumenidae) (Gess and Gess, 1976a and 1988b). The diameter of the turret of *Ceramius* species is in proportion to the size of the wasp (Gess and Gess, 1980) but is not constant for a species due to size variation between different populations of a species as has been shown for *C. lichtensteinii* (Gess and Gess, present paper).

To date perennial nests have been recorded for most species which construct mud-cells within excavated-cells but for none of the species which excavates cells but does not construct mud-cells within them.

Attention has been drawn (Gess and Gess, 1986) to the correlation between the nature of the cell and the length of secondary shafts. Based on a knowledge of the nesting of one species each from Group 3 and Group 5 and three species from Group 8 the observation was made that excavated cells in which mud-cells are not constructed (Group 8) seem to terminate long secondary shafts and cells in which mud-cells are constructed (Group 3 and Group 5) seem to terminate extremely short secondary shafts. The present observations concerning the nesting of *C. socius* (Group 8) which excavates relatively long secondary shafts each terminating in an excavated-cell in which a mud-cell is not constructed and of *C. cerceriformis* (Group 2) and *C. rex* (Group 6) both of which excavate relatively short secondary shafts each terminating in an excavated-cell in which a mud-cell is constructed add data to support the idea of the existence of a correlation.

The length of and arrangement of secondary shafts and cells combined with the nature of the turning "bulb", in fact the architecture of the burrow itself rather than that of the turret, characterize the species groups, there being considerable constancy of burrow plan within groups and variation between groups. Within the limitations of present knowledge it appears that Group 8 is distinct in having long secondary shafts and in the absence of a constructed cell within the excavated-cell. Group 5 is distinct in that the main shaft is not terminated by the first cell. Group 3 is distinct in that the cells are all excavated sub-vertically beneath the bulb. Group 2a and Group 6 are similar in that all the cells lie sub-horizontally in a group to one side of the lower end of the main shaft, the first cell terminating that shaft, however, they are distinguished by the nature of the "bulb". The bulb in Group 2a is, when present, short and at mid-length of the main shaft whereas that of Group 6 is relatively long and is positioned at or near the base of the main shaft.

Although the genus *Ceramius* has been shown to forage on several families of plants, Mesembryanthemaceae, Compositae and Leguminosae in the Afrotropical Region and

Leguminosae, Umbelliferae, Labiatae, Resedaceae and Plumbaginaceae in the Palaearctic Region, a considerable degree of oligolecty is exhibited at the species group and species levels. The four species of Group 3 have been recorded foraging and the provision of two of these species has been investigated. In all instances the flowers utilized were of the family Compositae only. *C. rex* one of the three species of Group 6 is recorded foraging on and provisioning with pollen from flowers of Compositae only. The four species of Group 8 have been recorded foraging on and provisioning with pollen from flowers of Mesembryanthemaceae only. The single species of Group 5 has been found to provision with pollen of Mesembryanthemaceae only. It is therefore of particular interest that the presently suggested division of Group 2 on morphological grounds is supported by differences in foraging preferences, the two species of Group 2a having been recorded foraging only on Mesembryanthemaceae and *C. clypeatus*, one of the two species of Group 2b, only on Leguminosae.

That *C. fonscolombei* and *C. bischoffi* have been recorded visiting flowers of more than one family is at present not given serious consideration as there is as yet no record of the nature of the pollen utilized. Records of casual plant visiting can be misleading. Although *C. lichtensteinii* has been collected on numerous occasions from flowers of "mesems" and samples of provision from cells were found to contain "mesem" pollen only the authors made a single record of this species visiting flowers of *Blepharis* sp. (Acanthaceae). It is therefore considered that "mesems" are the habitual forage plants of *C. lichtensteinii* and that the recorded visit to *Blepharis* sp. was casual in nature. The latter flowers are visited by a very wide range of insects, apparently for their nectar. This opinion is in keeping with that expressed by Cooper (1952) in a consideration of records of flower visiting by *Pseudomasaris* in North America.

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Gess, F. W. and Gess, S. K. 1975. Ethological studies of *Bembecinus cinguliger* (Smith) and *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae), two southern African turret building wasps. *Ann. Cape Prov. Mus. (nat. Hist.)* **11** (2): 21–46.

Gess, F. W. and Gess, S. K. 1976a. An ethological study of *Parachilus insignis* (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa. *Ann. Cape Prov. Mus. (nat. Hist.)* **11** (5): 83–102.

Gess, F. W. and Gess, S. K. 1976b. Ethological notes on *Dichragenia neavei* (Kohl) (Hymenoptera: Pompilidae), an African spider hunting wasp building a turreted. subterranean nest. *Ann. Cape Prov. Mus. (nat. Hist.)* **11** (8): 129–134.

Gess, F. W. and Gess, S. K. 1980. Ethological studies of *Jugurtia confusa* Richards, *Ceramius capicola* Brauns, *C. linearis* Klug and *C. lichtensteinii* (Klug) (Hymenoptera: Masaridae) in the Eastern Cape Province of South Africa. *Ann. Cape Prov. Mus. (nat. Hist.)* **13** (6): 63–83.

Gess, F. W. and Gess, S. K. 1986. Ethological notes on *Ceramius bicolor* (Thunberg), *C. clypeatus* Richards, *C. nigripennis* Saussure and *C. socius* Turner (Hymenoptera: Masaridae) in the Western Cape Province of South Africa. *Ann. Cape Prov. Mus. (nat. Hist.)* **16** (7): 161–178.

Gess, F. W. and Gess, S. K. 1988a. A contribution to the knowledge of the taxonomy and the ethology of the genus *Masarina* Richards (Hymenoptera: Masaridae). *Ann. Cape Prov. Mus. (nat. Hist.)* **16** (14): 351-362.

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Selected annotated bibliography of early developmental studies of African freshwater fishes

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INTRODUCTION

The Class Osteichthyes (bony fishes), with over 20 000 known species, has more anatomical diversity amongst the young than any other vertebrate class (Faber, 1985). On the African continent 74 families and some 2 000 freshwater fish are represented. Relatively little is known about the early life histories of these species.

Over the last decade there has been in many countries an increasing interest in early life history studies. However, for the African continent the literature is widely scattered and some good manuscripts remain unpublished. The aim of the present paper is to provide a selected annotated bibliography, which will clearly point out this important gap in the knowledge of the African ichthyofauna. This annotated list of references is selective. The papers or manuscripts which are included are on early development *sensu stricto*, where the identity of the species is substantiated. Those which include only growth rates or age determinations and those concerned with early stages solely for toxicity studies have not been included. As with any bibliography, there may be omissions, especially of unpublished manuscripts. It is planned to update this bibliography, possibly in five years time and workers are therefore encouraged to assist by letting the authors know of any omissions and future publications.

It is unfortunate that in all but a few papers (7 out of 153) mention is not made of the repository of the developmental series on which the authors have worked. The Department of Ichthyology at the Albany Museum has initiated a special collection of African freshwater fish early life history stages. Reference collections would be most welcome. They would be accessioned into the main collection. Many curators of adult fish collections are wary of microscopic specimens stored in vials. Their maintenance and documentation are labour intensive (Cohen, 1984). These early life history collections should be sent to organizations that have an institutional (not personal) commitment to long-term collection storage. The authors

have tried to trace some of the collections, but have had little success. It is desirable that an author include in his paper reference to the institution in which his collection has been lodged.

Early life history terminology can be confusing. In order to prevent further confusion, the terms used in most of the present annotations are the same as those used in the papers to which they refer. This point is noted to make readers aware of the presence of and reason for the inconsistencies in the use of terms in the annotations. It is recommended that in future workers should define clearly their use of early life history terminology or state which existing terminology they have used. For examples, see Balon (1975), Kendall *et al.* (1984) and Snyder (1981).

In the check-list of the freshwater fishes of Africa (CLOFFA) (Daget *et al.*, 1984 and 1986), early life history studies are usually not separated and are included under the terms biology or reproduction. The study of fish eggs, embryos and larvae sometimes forms an independent branch of fisheries biology, and it is suggested that it be given a separate listing in books of this nature. CLOFFA, gives a good indication of how little is known about the African ichthyofauna. For example out of a total of 292 *Barbus* species the biology and/or ecology of only 29 species are/is known. The early development of only nine species (<3%) has been described. For the 81 African *Labeo* species a similar picture emerges. The biology and/or ecology of 19 out of 81 species are/is known and only four early life history studies have been completed. Possibly one of the reasons why so few papers have been published on the early development of African freshwater fishes is that the eggs of freshwater fishes, unlike adult fishes, are rather difficult to collect. Once the developing eggs are collected, equipment and time are required to rear, collect and preserve a well documented developmental series. In contrast to the pelagic eggs of many sea fishes, many of the eggs of freshwater fishes are negatively buoyant and sink to the substratum, or are deposited in crevices, or are attached to plants or rocks by an adhesive membrane, or occur in the mouth of one parent. Many of the papers discuss development of eggs obtained by artificial reproduction of species important for aquaculture, and rarely is development followed under natural conditions, usually because of logistics and lack of equipment.

It has only been possible to locate early developmental studies for 18 of the 74 fish families in Africa. For phylogenetic studies the early stages offer a whole suite of characters not present in the adults, and further studies of the early period of development will add to the knowledge of fish interrelationships. Even within one species, the essence of development is change, and the characters that identify one stage will often not even exist in a later stage, eg. Kupffer's vesicle, finfolds, etc.

This bibliography should also be useful for those doing ecological studies in Africa. Early life and juvenile stages of fishes are considered sensitive indicators of ecological perturbations, such as pesticides, radioactive wastes, urban and industrial pollution and entrainment problems in power plants (Alderdice, 1985). In addition the lack of understanding of the early life history phase is still a major impediment to fish culture (Hempel, 1979), similarly to the management of natural stocks. An understanding of the ecology of the early life history stages of fishes is essential for answering certain practical questions with regard to exploitation of fish populations.

In the format for each reference author(s), date, title and source are included when available. In the annotation a brief abstract is given, the presence of photomicrographs or camera-lucida illustrations is noted and museum collection numbers are cited when possible.

REFERENCES FOR INTRODUCTION

Alderdice, D. F. 1985. A pragmatic view of early life history studies of fishes. *Trans. Am. Fish. Soc.* **114:** 445–451.
Balon, E. K. 1975. Terminology of intervals in fish development. *J. Fish. Res. Bd Can.* **32:** 1663–1670.
Cohen, D. M. 1984. Ontogeny, Systematics, and Phylogeny. In: Moser, H. G. *ed. Ontogeny and Systematics of Fishes*. Special Publication. Am. Soc. of Ichthyologists and Herpetologists. Lawrence: Allen. pp. 7–11.
Daget, J., Gosse, J. P. and Thys van den Audenaerde, D. F. E. 1984. *Check-list of the freshwater fishes of Africa*. Vol. 1. ORSTOM (PARIS), MRAC (TERVUREN). 410pp.
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Faber, D. J. 1985. Book review. *ELHS, A.F.S. newsletter* **6**(1): 18.
Hempel, G. 1979. *Early life history of marine fish*. Seattle: Univ. of Washington Press. 70pp.
Kendall, A. W. jr., Ahlstrom, E. H. and Moser, H. G. 1984. Early life history stages of fishes and their characters. In: Moser, H. G. *ed. Ontogeny and systematics of fishes*. Special Publication, Am. Soc. of Ichthyologists and Herpetologists. Lawrence: Allen. pp. 11–22.
Snyder, D. E. 1981. Contributions to a guide to the cypriniform fish larvae of the upper Colorado River System. *U.S. Dep. Inter. Bur. Land and Manage. Colo. Off. Biol. Sci Ser.* 3, 81pp.

SELECTED PAPERS BY FAMILY

PROTOPTERIDAE

Agar, W. E. 1906. The development of the skull and visceral arches in *Lepidosiren* and *Protopterus*. *Trans. R. Soc. Edinb.* **45:** 49–64, 16 figs, 3 pls.

The development of the skull and the visceral arches in *Protopterus* sp. (= *Protopterus annectens*) from the Gambia River is described and illustrated with camera lucida drawings.

Agar, W. E. 1907. The development of the anterior mesoderm and paired fins with their nerves in *Lepidosiren* and *Protopterus*. *Trans. R. Soc. Edinb.* **45:** 611–639.

Protopterus sp. (= *Protopterus annectens*) development is described as per title and illustrated with camera lucida drawings.

Brien, P. 1959. Ethologie du *Protopterus dolloi* (Boulenger) et de ses larves. Signification des sacs pulmonaires des Dipneustes. *Annls Soc. r. zool. Belg.* **89:** 9–48, 10 figs.

Eggs, embryos and larvae, from the hatching stage (19,6 mm) up to the fifteen day old swimming larvae (25,1 mm) of *Protopterus dolloi*, are drawn, described and compared to *Protopterus annectens*. The ontogeny of respiratory organs is included.

Brien, P. and Bouillon, J. 1959. Ethologie des larves de *Protopterus dolloi* et études de leurs organes respiratoires. Résultats scientifiques d'une mission zoologique CEMUBAC au Stanley Pool, subsidiée par l'ULB et le MRCB. *Annls Mus. r. Congo belge Sér.* **8**(71): 25–74, pls 7–11, 38 figs.

The development of *Protopterus dolloi* from the Malebo Pool (Zaire) is described and compared to that of *P. annectens*, from the hatched larvae (19,6 mm) up to the 25,1 mm larva. Illustrations are as in Brien, 1959.

Budgett, J. S. 1900. On the breeding habits of some West African fishes with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Proc. zool. Soc. Lond.*: 835–6. Also in: Kerr, G. *ed.*, *Budgett Memorial Volume*, 1907. Cambridge: Univ. Press.

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Trans. zool. Soc. Lond.* **16**(2): 115–132, 5 figs, 2 pls.

External features in the development of wild collected *Protopterus annectens* from the Gambia River are illustrated using graphical reconstructions from the cleavage egg up to the small adult with brief descriptions. Comparison of development of *Protopterus* with *Lepidosiren* is included.

Budgett, J. S. 1901b. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104. Also in: Kerr, G. *ed.*, *Budgett Memorial Volume*, 1907, Cambridge: Univ. Press. pp. 141–142.

The eggs and larvae of *Protopterus annectens* from the Gambia River are briefly described.

Kerr, J. G. 1901. The development of *Lepidosiren paradoxa, with a note upon the corresponding stages in the development of* Protopterus annectens (Protopteridae). *Q. Jl. microsc. Sci.* **2**(45): 1–40, 4 pls.

Not seen.

Kerr, J. G. 1909. Normal plates of the development of *Lepidosiren paradoxa* and *Protopterus annectens*. *Norm Taf. EntwGesch. Wirbeltiere* **3:** 1–31.

Not seen.

Kerr, J. G. 1910. On certain features in the development of the alimentary canal in *Lepidosiren* and *Protopterus*. *Q. Jl microsc. Sci.* **54:** 483–518.

Not seen.

Pasteels, J. 1962. Résultats scientifiques des Missions zoologiques au Stanley Pool subsidiées par le CEMUBAC (Université Libre de Bruxelles) et le Musée Royal du Congo Belge (1957–1958). XII. Gastrulation du *Protopterus dolloi*. *Annls Mus. r. Afr. centr. Sér.* **8**(108): 173–183, 3 pls.

The gastrulation in *Protopterus dolloi* from the Malebo Pool in Zaire, is described in detail and illustrated with camera lucida drawings and photographs.

Svensson, G. S. O. 1933. *Freshwater fishes from the Gambia River (British West Africa):* Results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

General data on eggs and larvae of *Protopterus annectens* are given.

POLYPTERIDAE

Abdel-aziz, I. A. 1957. Notes on the anatomy of larval *Polypterus*. *Proc. Egypt. Acad. Sci.* **12:** 79–87, 12 figs.

Anatomical features of larval *Polypterus senegalus* from Bahr El-Zaraf, Upper Nile Province, Sudan, using serial sections and graphic reconstructions on digestive and urino-genital systems are described. Illustrations of transverse sections are included.

Arnoult, J. 1962. Ponte naturelle suivie d'éclosions chez *Polypterus senegalus senegalus* (Cuvier). *C.r. Séanc. Acad. Sci.* (Paris) **254:** 2828–2829.

After *Polypterus senegalus senegalus* spawned in the Upper Volta, the eggs and early larval stages were collected and described. There are no illustrations.

Arnoult, J. 1964. Comportement et reproduction en captivité de *Polypterus senegalus* (Cuvier). *Acta zool., Stockh.* **46:** 191–199, 3 figs.

The development of *Polypterus senegalus* collected from the Upper Volta basin and reared in an aquarium was followed. Photographs of the 41 hour old fertilized egg, the 54 hour old larvae and the 20 day old juvenile are included.

Budgett, J. S. 1900. On the breeding habits of some West African fishes with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei. Proc. zool. Soc. Lond:* 835–6.

Larvae of *Polypterus lapradei* (= *Polypterus senegalus)* are described.

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei. Trans. zool. Soc. Lond.* **16**(2): 115–132, 5 figs, 2 pls.

The larvae of *Polypterus lapradei* (= *Polypterus senegalus)* are described and illustrated with drawings.

Budgett, J. S. 1901b. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104. Also in: Kerr, G. *ed. Budgett Memorial Volume*—1907. Cambridge: Univ. Press, pp. 141–142.

A larva of *Polypterus,* 30 mm length, from the Gambia River is described.

Budgett, J. S. 1902a. On the structure of larval *Polypterus. Trans. Zool. Soc. Lond.* **16**(7): 315–340, 3 pls, 5 figs. Also in: Kerr, G. *ed. Budgett Memorial Volume*—1907. Cambridge: Univ. Press, pp. 141–142.

Transverse sections of a larva of *Polypterus* (30 mm) from the Gambia River, double stained with haemotoxyline and eosine and drawn from reconstructions by Kerr's method (camera lucida) are described. An account is given of the structure of the cartilaginous skeleton and subsequent development as studied in a number of specimens from 9 cm upwards. The genital and excretory system in this larva are described.

Budgett, J. S. 1902b. On the anatomy of larval *Polypterus. Rep. Br. Ass. Advmt Sci.* **71:** 693.

The osteology and the anatomy of a larval specimen of *Polypterus* (30 mm length) from the Gambia River are briefly described. No illustrations are included.

Daget, J., Bauchot, M. L. and R. and Arnoult, J. 1964. Développement du chondrocrâne et des arcs aortiques chez *Polypterus senegalus* Cuvier. *Acta zool., Stockh.* **45:** 201–244, 34 figs.

Organogenesis of the chondrocranium and the aortic arches in *Polypterus senegalus* from 4,5 mm up to 22,5 mm from Upper Volta is described. Graphic reconstructions based on photographs are included in this paper.

Guitel, F. 1914. Contribution à l'étude d'une larve de *Polypterus senegalus* Cuvier de 59 mm de longueur. *Archs Zool. exp. gén.* **54**(12): 411–437, 12 figs, 2 pls.

A 59 mm larvae of *Polypterus senegalus* from Lake Chad is described in detail (external morphology) and compared to other species of the genus. Illustrations are included.

Johnels, A. G. 1954. Notes on fishes from the Gambia River. *Ark. Zool.* **6**(17): 326–411, 19 figs.

The development of *Polypterus senegalus*(?) is briefly described and two photographs of a 10 mm TL larva are included.

Jungersen, H. F. E. 1895. Ueber die Embryonalniere von *Calamoichthys calabaricus* (Smith) von J. Lebedinsky. *Zool. Zentbl.* **2:** 54–59.

Not seen.

Kerr, J. G. 1904. Note on the developmental material of *Polypterus* (Polypteridae) obtained by the late Mr. J. S. Budgett. *Rep. Br. Ass. Advmt Sci.* **74:** 604–605.

Not seen.

Kerr, J. G. 1907a. The development of *Polypterus senegalus* Cuv. In: Kerr, G. *ed. Budgett Memorial Volume*—1907. Cambridge: Univ. Press, pp. 195–284.

Developmental material of *Polypterus senegalus*, collected by Budgett, is investigated by means of paraffin sections. Drawings and descriptions of the external development of early cleavage eggs, embryos and larvae are given. Detailed internal features of development are described and drawn, from gastrulation to larval fish, including development of mesoderm, notochord, alimentary canal, cement organs, excretory organs, vascular system, cartilaginous skeleton and the nervous system.

Kerr, J. G. 1907b. The development of *Polypterus senegalus* Cuv. *Proc. R. phys. Soc. Edinb.* **17**(2): 73–5.

Not seen.

Nieuwenhuys, R., Bauchot, R. and Arnoult, J. 1969. Le développement du télencéphale d'un poisson osseux primitif, *Polypterus senegalus* Cuvier. *Acta zool., Stockh.* **50:** 101–125, 29 figs.

The development of the forebrain in *Polypterus senegalus* has been studied from the 5,5 mm larvae up to a 28 mm juvenile. Photographs of transverse and horizontal sections are given for the different stages examined. The forebrain in adult specimens of the same species is described.

Svensson, G. S. O. 1933. Fresh-water fishes from the Gambia River (British West Africa): results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

General data on eggs and larvae of *Polypterus lapradei* (= *Polypterus bichir lapradei*) and *Polypterus senegalus* are given.

CLUPEIDAE

Aigner, T. and Laurent, M. 1976. Note sur les alevins de *Stolothrissa tanganicae* et de *Limnothrissa miodon* au Burundi. *FAO, Fish. Res. Rep. BDI/73/020, working paper nr. 9.*

Not seen.

Albaret, J. J. and Gerlotto, F. 1976. Biologie de l'ethmalose (*Ethmalosa fimbriata* Bowdich) en Côte d'Ivoire. I. Description de la reproduction et des premiers stades larvaires. *Doc. scient. Cent. Rech. océanogr. Abidjan.* **7**(1): 113–133, 12 figs.

The larval development of *Ethmalosa fimbriata* from Ebrie Lagoon, Ivory Coast, from the unfertilized egg up to the vitelline vesicule resorption stage is described in detail. This paper includes drawings and photographs.

Bainbridge, V. 1957. Eggs and larvae of *Ethmalosa dorsalis*. Cons. Scient. Afr., Symp. Luanda 1957.

The eggs and larvae of *Ethmalosa dorsalis* (= *Ethmalosa fimbriata*) are briefly described.

Bainbridge, V. 1960. The early life history of the Bonga, *Ethmalosa dorsalis* (Cuvier & Valenciennes). *J. Cons. Perm. Int. Expl. Mer* **26**(1): 347–353, 2 figs.

The development of the eggs and larvae of *Ethmalosa dorsalis* (= *Ethmalosa fimbriata*) from the Sierra Leone River, Sierra Leone, is described. The following stages are drawn: egg two hours and fifteen hours after fertilization, newly hatched larva, yolk-sac larva twenty four hours after hatching, larva 60 hours after hatching.

Bainbridge, V. 1962. The larvae of *Pellonula vorax* Günther (Clupeidae) in Sierra Leone coastal waters. *Bull. Inst. fr. Afr. noire* (A) **24** (1): 262–269, 4 figs.

Larvae of *Pellonula vorax* from the Sierra Leone River, Sierra Leone, covering the complete size range (6 to 17,9 mm SL) are described externally. Camera lucida drawings are included.

Conand, F. 1977. Oeufs et larves de la sardinelle ronde (*Sardinella aurita*) au Sénégal: distribution, croissance, mortalité, variations d'abondance de 1971 à 1976. *Cah. ORSTOM, océanogr.* **15**(3): 201–214, 13 figs.

Six to 12 mm larvae of *Sardinella aurita* were collected using Bongo nets off the Senegalese coast. These stages are briefly described.

Conand, F. and Fagetti, E. 1971. Description et distribution saisonnière des larves de Sardinelles des côtes du Sénégal et de la Gambie en 1968 et 1969. *Cah. ORSTOM, océanogr.* **9**(3): 293–318, 17 figs.

Morphological and biometrical observations on 5 to 15 mm larvae of *Sardinella aurita* and *S. eba* (= *S. maderensis*) from the Senegalese coasts are given. For both species drawings of the larval development are included (larvae smaller than 6 mm; larvae between 6 and 11 mm; larvae between 11 and 15 mm; larvae between 16 and 20 mm).

Dessier, A. 1969. Note sur les stades larvaires et post larvaires d'*Ilisha africana* (Bloch, 1795) (Pisces; Clupeidae). *Cah. ORSTOM, océanogr.* **7**(4): 21–25, 3 figs, 2 pls.

This paper includes descriptions and drawings of larval (5,7 up to 12,4 mm SL), postlarval (15,5 up to 21,8 mm SL) and juvenile stages (31,5 mm SL) of *Ilisha africana* caught off the coasts of Congo and Gabon.

Johnels, A. G. 1954. Notes on fishes from the Gambia River. *Ark. Zool.* **6**(17): 326–411, 19 figs.

Biometrical features of the larvae of *Pellonula afzeliusi, up to 30 mm TL, are given.*

Marchal, E. G. 1967. Clé provisoire de détermination des oeufs et larves des Clupéides et Engraulides Ouest-Africains. *ORSTOM, Docums scient. Provis.* 14, 4 pp., 10 figs.

This paper provides provisionary identification keys for Clupeidae and Engraulidae eggs and larvae from the coasts of Senegal to Congo. Drawings of the egg and the 5,2, 9,2, 19,6 and 23,9 mm larvae of *Sardinella aurita*, the egg and the 10,4 and 19,2 mm larvae of *Sardinella eba* (= *S. maderensis*), the egg and the 5,1 mm larva of *Harengula rouxi*, the egg of *Ethmalosa fimbriata* and *Ilisha africana* are included.

Svensson, G. S. O. 1933. Fresh-water fishes from the Gambia River (British West Africa): Results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

General data on eggs and larvae of *Pellonula vorax* (= *Sierrathrissa leonensis* + *Pellonula* spp.) are given.

Teugels, G. G. and Thys van den Audenaerde, D. F. E. 1979. A morphological and anatomical study of *Pellonula afzeliusi* Johnels, 1954 and *Sierrathrissa leonensis* Thys, 1969 (Pisces; Clupeidae). *Rev. zool. afr.* **93**(3): 523–538, 10 figs.

Morphological and osteological comparisons between growth series of *Pellonula afzeliusi* (16,2–58,6 mm SL) and *Sierrathrissa leonensis* (9,8–30,4 mm SL) from West Africa are given. Camera lucida drawings of alizarin stained specimens are included.

Whitehouse, R. H. 1933. Report on fish eggs and larvae taken during 1931. *Notes Mem. Fishery Res. Dir., Cairo* **4**: 1–22, 20 figs.

Larval stages in *Sardinella aurita* from the Nile (2,3 mm up to 6,5 mm) are described. Drawings of the 3,2 mm, 4,6 mm and the 5,9 mm larvae are included.

OSTEOGLOSSIDAE

Assheton, R. 1907. Report upon sundry Teleostean eggs and larvae from the Gambia River. In: Kerr, G. *ed.*, *Budgett Memorial Volume—1907.* Cambridge: Univ. Press, pp. 433–442, 6 figs.

This paper includes data from eight larval stages and drawings of the caudal fin development of *Heterotis niloticus* from the Gambia River. A drawing and description of a yolk-sac larva as well as drawings of transverse sections of forebrain and epiphysis are included.

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Trans. zool. Soc. Lond.* **16**(2): 115–132, 5 figs, 2 pls. Also in: Kerr, G. *ed. Budgett Memorial Volume—1907.* Cambridge: Univ. Press, pp. 119–136.

The larva, one day after hatching, of *Heterotis niloticus* is drawn and described.

Budgett, J. S. 1901b. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104.

This paper includes a brief description of and data on eggs and larvae of *Heterotis niloticus*.

Daget, J. 1957. Mémoires sur la biologie des poissons du Niger Moyen. III. Reproduction et croissance d'*Heterotis niloticus* Ehrenberg. *Bull. Inst. fr. Afr. noire* **19**(1): 295–323, 3 figs, 2 pls.

The development of the eggs and the larvae of *Heterotis niloticus* from the Central Niger is described. This paper includes detailed discussions and camera lucida drawings from stage I (larva just after hatching—7,5 mm TL) up to stage X (larva 8 days after hatching—14 mm TL).

Daget, J. and D'aubenton, F. 1957. Développement et morphologie du crâne d'*Heterotis niloticus*. *Bull. Inst. fr. Afr. noire* **19**(3): 881–936, 31 figs.

The cranial development (neurocranium, splanchnocranium and dermal cranium) and the morphology of *Heterotis niloticus* from the Central Niger, from stage I (hatching—7,5 mm TL) up to stage X (8 days after hatching—14 mm TL) using longitudinal serial sections, stained after Mallory are described. Illustrations of sections are included.

Olaniyan, C. I. O. and Zwilling, K. K. 1963. The suitability of *Heterotis niloticus* Ehrenbaum (Osteoglossidae) as a fish for cultivation: with a note on its spawning behaviour. *Bull. Inst. fr. Afr. noire* **25**(2): 513–525.

A short account is given of the spawning behaviour of *Heterotis niloticus* under fish pond conditions in Panyam, Northern Nigeria. Reference is made to Daget (1957) for the first week of development. No illustrations are included.

Svensson, G. S. O. 1933. Fresh-water fishes from the Gambia River (British West Africa): Results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl* **12**(3): 1–102, 28 figs, 8 pls.

General data on eggs and larvae of *Heterotis niloticus* are described, including the drawings of three stages, 12,5, 14,0 and 27,0 mm.

NOTOPTERIDAE

Svensson, G. S. O. 1933. Fresh-water fishes from the Gambia River (British West Africa): Results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

This paper includes general data on eggs and larvae of *Notopterus afer* (= *Papyrocranus afer)*.

MORMYRIDAE

Daget, J. 1958. Alevins de *Mormyrus rume* C. & V.. *Bull. Soc. zool. Fr.* **83**(2–3): 200–204, figs 1–3.

A description of external morphological development of *Mormyrus rume* from the Central Niger, based on ten larvae from 10 mm (just after the resorption of the yolk sac) up to 26 mm TL is outlined. Seven specimens are illustrated.

Fritsch, G. T. 1892. On the origin of the electric nerves in the torpedo, *Gymnotus*, *Mormyrus* and *Malapterurus*. *Rep. Br. Ass. Advmt Sci.*: 757–788.

Not seen.

Johnels, A. G. 1954. Notes on fishes from the Gambia River. *Ark. Zool.* **6**(17): 326–411, 19 figs.

Biometrical features of several larval and juvenile stages of *Mormyrops deliciosus* (18,2 to 430 mm SL) are tabulated. Detailed descriptions and camera lucida drawings of developmental stages (from stage I, being the newly hatched embryo—4,5 mm SL up to stage VII, being the nine day old larva—6,2 mm SL) of *Hyperopisus bebe* are included.

Szabo, T. 1960. Development of the electric organ of Mormyridae. *Nature, Lond.* **188**(4752): 760–762.

Not seen.

Westby, G. W. M. and Kirschbaum, F. 1977. Emergence and development of the electric organ discharge in the mormyrid fish, *Pollimyrus isidori*. I. The larval discharge. *J. comp. physiol.* **122:** 251–271.

The development of the electric organ discharge in the mormyrid fish, *Pollimyrus isidori* is described. Laboratory bred larvae were monitored. A photograph of an eight day old specimen is included.

GYMNARCHIDAE

Assheton, R. 1907. The development of *Gymnarchus niloticus*. In: Kerr, G. *ed*. *Budgett Memorial Volume—1907*. Cambridge: Univ. Press, pp. 293–432, 79 figs.

The external morphology of several developmental stages of *Gymnarchus niloticus* from the Gambia River is described in detail and is illustrated from the egg to the juvenile period (fortieth day). The development of the alimentary canal, the vascular system, the reproductive organs, the excretory organs, the nervous system and the skeleton is described, including drawings of sagittal and transverse sections of various stages.

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Trans. zool. Soc. Lond.* **16**(2): 115–132, 5 figs, 2 pls. In: Kerr, G. *ed. Budgett Memorial Volume*—1907. Cambridge: Univ. Press, pp. 119–136, 2 pls.

This paper includes descriptions and drawings of the larvae of *Gymnarchus niloticus*, between two and six days after hatching.

Budgett, J. S. 1901. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104. Also In: Kerr, G. *ed. Budgett Memorial Volume—1907* Cambridge: Univ. Press, pp. 119–136, 2 pls.

Brief descriptions of the eggs and larvae of *Gymnarchus niloticus* from the Gambia River are given.

Dahlgren, U. 1910. The origin of electric tissues in fishes. *Am. Nat.* **44:** 193–202.

The ontogeny of the electric organ in *Gymnarchus niloticus* is described from the ninth day embryo to the stage between the twelfth and the fourteenth day. No illustrations are included. These specimens were collected by Budgett.

Dahlgren, U. 1914a. Origin of the electric tissues of *Gymnarchus niloticus*. *Publs Carnegie Instn* **183:** 159–194.

Not seen.

Dahlgren, U. 1914b. Embryonic history of the electric apparatus in *Gymnarchus niloticus*. *Proc. int. Congr. Zool.* **9:** 379.

Not seen.

Srivastava, C. B. L. and Szabo, T. 1972. Development of electric organs of *Gymnarchus niloticus* (Fam. Gymnarchidae). 1 Origin and histogenesis of electroplates. *J. Morph.* **138**(3): 375–386.

The authors used a fairly complete series of embryonic stages of *Gymnarchus niloticus* collected from Dia farabe, Mali. Material included recently hatched free embryos and following stages to complete absorption of the yolk. A table is included which indicates the developmental characters for 17 stages. The development of the electric organs was studied and the origin and histogenesis of an electroplate is described. One photograph of a fry of approximately 3,5 days after hatching is included. The paper also includes photomicrographs of sagittal and transverse sections of the tail at various developmental stages.

Srivastava, C. B. L. and Szabo, T. 1973. Development of electric organs of *Gymnarchus niloticus* (fam. Gymnarchidae). *J. Morph.* **140**(4): 461–465.

The development of the electric organ spindles of *Gymnarchus niloticus* was investigated with regard to the exact time and place of origin. Photomicrographs of transverse and sagittal sections of the tail at several stages of development are included.

Svensson, G. 1933. Fresh-water fishes from the Gambia River (British West Africa): Results of the Swedish expedition 1931. *K. svenska VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

General data on eggs and larvae of *Gymnarchus niloticus* are included.

HEPSETIDAE

Bertmar, G. 1959. On the ontogeny of the chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta zool., Stockh.* **40**(2–3): 203–364, 85 figs.

The ontogeny of the chondrocranium of *Hepsetus odoë* from the Gambia River is described, based on a large collection of embryological material consisting of seventy stages from the egg up to a 45 mm juvenile, using graphical reconstructions based on photographs. The results are compared to those for *Alestes nurse* (Characidae), *Citharinus citharus* (Citharinidae), *Distichodus brevipinnis* (Distichodontidae), *Distichodus rostratus* (Distichodontidae), *Nannaethiops unitaeniatus* (Distichodontidae), *Nannocharax ansorgii* (Distichodontidae), *Protopterus annectens* (Protopteridae), *Polypterus senegalus* (Polypteridae) and *Heterotis niloticus* (Osteoglossidae). The material examined, is housed in the Zootomical Institute, University of Stockholm, Sweden.

Bertmar, G. 1962. On the ontogeny and evolution of the arterial vascular system in the head of the African Characidean fish *Hepsetus odoë*. *Acta zool., Stockh.* **43:** 255–294, 12 figs.

As per title on 70 specimens (6,5–45,0 mm) of *Hepsetus odoë* from the Gambia River, using graphic reconstructions based on photographs. The series are housed in the Zootomical Institute, University of Stockholm, Sweden.

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Trans. zool. Soc. Lond.* **16**(2): 115–132, 5 figs, 2 pls.

This paper includes descriptions and drawings of the larvae of *Sarcodaces odoë* (= *Hepsetus odoë*) just after hatching.

Budgett, J. S. 1901b. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104.

Brief descriptions and data of the eggs and larvae of *Sarcodaces odoë* (= *Hepsetus odoë*) from the Gambia River are given.

Svensson, G. S. O. 1933. Fresh-water fishes from the Gambia River (British West Africa): Results of the Swedish expedition 1931. *K. svenska. VetenskAkad. Handl.* **12**(3): 1–102, 28 figs, 8 pls.

The foam nest, eggs and larval behaviour of *Hydrocyonoides odoë* (= *Hepsetus odoë*) are briefly described. These stages are not illustrated, but the author agrees with larva pictured by Budgett (Kerr, 1907, Plate IX), and large adhesive organ described by Budgett (1901).

CHARACIDAE

Abdel-Aziz, I. 1961. The chondrocranium of *Hydrocyon forskalii* larva (9 mm). II. Branchial arches. *Proc. Egypt. Acad. Sci.* **15:** 65–69.

Osteological features of branchial arch development in 6,5 mm and 9,0 mm larvae of *Hydrocyon forskalii* (= *Hydrocynus forskalii*) from the Nile are described. This paper is not illustrated.

Bowmaker, A. P. M. 1973. *An hydrobiological study of the Mwenda River and its mouth, Lake Kariba*. Unpubl. Ph.D. thesis, Univ. of Witwatersrand.

Ripe and running wild collected *Hydrocynus vittatus* were stripped of gametes. Development was followed at 24–25°C under laboratory conditions. Development is described from cleavage egg, to a late larval stage at 35 days after fertilization. Illustrations of middle gastrula, late gastrula, various embryonic stages, including free embryos and larval stages are included. Larval behaviour and pigmentation is given. Specimens are lodged at the National Museum and Monuments, Bulawayo, Zimbabwe and at Albany Museum, Grahamstown, South Africa, (AMG/P 11187).

Durand, J. R. 1978. Biologie et dynamique des populations d'*Alestes baremoze* (Pisces; Characidae) du bassin Tchadien. *Trav. Doc. ORSTOM,* **98:** 1–332.

This paper includes the biology and population dynamics of *Alestes baremoze* from the Tchad Basin, with a section on the reproduction and the early development of this species. The ripe eggs, the larvae just after hatching, the 4 day old larva and the one month old larva are described in detail. A 4 day old yolk-sac larva and a 30 day old juvenile are illustrated with camera lucida drawings.

Durand, J. R. and Loubens, G. 1970. Observations sur la sexualité et la reproduction des *Alestes baremoze* du bas Chari et du lac Tchad. *Cah. ORSTOM, hydrobiol.* **4**(2): 61–81, 9 figs.

This paper includes a brief description of the eggs of *Alestes baremoze* from Lake Chad and Lower Chari Basin.

Durand, J. R. and Loubens, G. 1971. Développement embryonnaire et larvaire d'*Alestes baremoze*. *Cah. ORSTOM, hydrobiol.* **5**(2): 137–145, 8 figs.

The embryonic and larval development of *Alestes baremoze* from Lake Chad is studied from artificially fertilized eggs which were aquarium reared. Drawings of and data on the embryo in segmentation, in gastrulation and just before hatching are included. Descriptions and drawings of a 21 hour larva (3,5 mm TL), a 4 day larva (5,6 mm TL), a 15 day larva (15 mm TL) and a juvenile of 30 days (17,5 mm TL) are given.

NEUMANN, M. 1968. Die Zucht von *Phenacogrammus interruptus*—ein Rätsel. *Aquar.-u.Terrar.-Z.* **21:** 136–139, 5 figs.

Descriptions and photomicrographs of the eggs of *Phenacogrammus interruptus* up to twelve hours before hatching were based on aquarium reared fish.

CYPRINIDAE

BALON, E. K., DUYVENE DE WIT, J. J. and HOLCIK, J. 1962. The early stages of development of the intersubfamiliar hybrid *Puntius anoplus/Rhodeus ocellatus* (Cyprinidae). *Zool. Anz.* **168**(1–4): 102–112.

This paper includes one figure and a brief description of *Puntius anoplus* (= *Barbus anoplus*) protopterygiolarva (4,8 mm TL).

BARNARD, K. H. 1943. Revision of the indigenous freshwater fishes of the S W Cape region. *Ann. S. Afr. Mus.* **36**(2): 101–262.

A brief description and morphometric and meristic table of *Labeo capensis* 16 mm to 450 mm TL are given. One drawing of a 16 mm TL late larvae is included. Lateral views of 9,5, 10,5, 12 and 15 mm TL larva of *Labeo seeberi* are illustrated. The author also gives some morphometrics and a short description. There is some doubt as to the proper identification of these wild collected specimens. The lateral view of a 14 mm *Barbus andrewi* larval fish is illustrated and a morphometric-meristic table for fish from 12 mm to 525 mm TL is included. There is a morphometric-meristic table of larval *Barbus asper* from 7–8 mm TL. The lateral view of a 13 mm TL *Barbus burchelli* larval fish is illustrated. The lateral view of a 13 mm TL *Barbus callidus* is illustrated and a morphometric and meristic table for fish from 11 mm to 93 mm TL is included. Lateral views of a 15 mm TL larval fish and a 23 mm juvenile of *Barbus capensis* are illustrated. A morphometric and meristic table is included.

CAMBRAY, J. A. 1983. Early development and larval behaviour of a minnow, *Barbus anoplus* (Pisces; Cyprinidae). *S. Afr. J. Zool.* **18:** 331–336.

This is the first known study of the development of an African barb, *Barbus anoplus*. Tables and camera lucida drawings of development from fertilized ova to juvenile fish are included. Development was followed for 13 months. The paper includes egg and larval behaviour and a description of the pigmentation of the various stages. The developmental series is housed at the Albany Museum, Grahamstown, South Africa, (AMG/P 9259).

CAMBRAY, J. A. 1985. Early ontogeny of *Labeo capensis* (Pisces: Cyprinidae). *S. Afr. J. Zool.* **20:** 190–196.

The early development of *Labeo capensis* is described from wild-spawned, laboratory reared specimens, which were followed for 5 months. Illustrations of early embryos (6), larval fish (7) and the juvenile stage are included. Meristic and morphometric tables are included for specimens from 5 mm to 40 mm TL. A table is included comparing *L. capensis* developmental stage sizes with other *Labeo* species. Specimens are lodged at the Albany Museum, Grahamstown, South Africa, (AMG/P 10125).

CAMBRAY, J. A. 1985. Early development of an endangered African barb, *Barbus trevelyani* (Pisces: Cyprinidae). *Rev. Hydrobiol. trop.* **18**(1): 51–60.

Barbus trevelyani were artificially induced to spawn. Eggs were fertilized and their development is recorded through the embryonic, larval and juvenile stages. Meristic 3–30 mm TL and morphometric 3–38 mm TL tables are included. Camera lucida drawings of 8 larval stages and 3 juvenile stages are included. Specimens are lodged at the Albany Museum, Grahamstown, South Africa, (AMG/P 10135 and 10136).

CAMBRAY, J. A. and MEYER, K. (in press). Early ontogeny of an endangered, relict, cold-water cyprinid from Lesotho, *Oreodaimon quathlambae* (Barnard, 1938). *Rev. Hydrobiol. trop.*

The early development of *Oreodaimon quathlambae* is described from wild-collected specimens. Illustrations of early embryos, larval fish and the juvenile stage are included. Meristic and morphometric tables are included for specimens 5–40 mm TL. Developmental osteogenesis is described. Specimens are lodged at the Albany Museum, Grahamstown, South Africa, (AMG/P 11224).

FRYER, G. and WHITEHEAD, P. J. P. 1959. The breeding habits, embryology and larval development of *Labeo victorianus* Boulenger (Pisces; Cyprinidae). *Revue Zool. Bot. afr.* **59**(1–2): 33–49, 24 figs.

The embryos and larvae of *Labeo victorianus* from Lake Victoria, from the fertilized egg up to the juvenile period (37 days) are described in detail and illustrated with camera lucida drawings.

GAIGHER, I. G., NTLOKO, M. M. and VISSER, J. G. 1975. Reproduction and larval development of *Labeo umbratus* (Pisces: Cyprinidae) in the Tyume River, Eastern Cape. *J. Limnol. Soc. sth. Afr.* **1**(1): 7–10.

Larval *Labeo umbratus* which were collected in the wild are briefly described. Four illustrations, one of late embryonic, newly hatched, 3 and 12 days after hatching (20–23°C) are included.

GROENEWALD, A. A. v. J. 1961. A progress report on the culture of *Barbus holubi*, the Vaal River yellowfish, at the provincial fisheries institute, Lydenburg. *Res. Rep. Prov. Fish. Inst. Tvl Prov. Admin.* Pretoria, 19pp.

Fertilized eggs (n=150) of *Barbus holubi* (= *B. aeneus*) at the sixteen celled stage were collected from a breeding pond. The author gives a description of the eggs and larvae up to the 13 mm stage (19 days). Drawings of embryos and larvae are included. Larval behaviour is described.

MITCHELL, S. A. 1984. Further observations on the breeding behaviour of *Labeo umbratus* (Smith) (Pisces: Cyprinidae). *J. Limnol. Soc. sth. Afr.* **10**(1): 28–30.

This paper includes a brief description of egg and larval behaviour. No illustrations are included.

VAN DER MERWE, F. J. 1981. Induced spawning of the common carp and Aischgrund carp

(*Cyprinus carpio*) and the largemouth yellowfish (*Barbus kimberleyensis*). *Water SA* **7**(2): 107–109.

A very brief account of hatching and larval behaviour of *Barbus kimberleyensis* is given.

Van der Westhuizen, T. F. 1974. *Die ontogenese van die viscerocranium van* Barbus holubi *Steindachner (Cyprinidae)*. M.Sc. thesis, Rand Afrikaans Univ.

The development of the viscerocranium of *Barbus holubi* (= *B. aeneus*) is described in detail. Illustrations and descriptions for the following stages are included; 8 mm TL (3 days), 9,5 mm TL (12 days), 13,5 mm TL (27 days), 21 mm TL (45 days) and 24 mm TL (55 days). Stages were microtomized and stained.

Van der Westhuizen, T. F. 1979. *Die ontogenese van die neurocranium van* Barbus holubi *Steindachner (Cyprinidae) met spesiale verwysing na die inkorporering van viscerale elemente in die neurocranium*. Unpublished Ph.D. thesis, Rand Afrikaans Univ.

The development of the neurocranium including the procartilagenous developmental stages is described for *Barbus holubi* (= *B. aeneus*). Fourteen developmental stages were microtomized at a thickness of 10μ. Seven developmental stages were described using drawings and reconstructions made from transverse sections; 7,5 mm TL (48h), 8,0 mm TL (3 days), 9,25 mm TL (6 days), 10,0 mm TL (10 days), 10,5 mm TL (20 days), 13,5 mm TL (27 days) and 21,0 mm TL (45 days). Special attention was given to the ontogenesis of the *commissura palatoquadrati*.

Welcomme, R. L. 1969. The biology and ecology of the fishes of a small tropical stream. *J. Zool.* **158:** 485–529, 18 figs.

Artificially fertilized eggs of *Barbus kerstenni* from the Kafunta River, Uganda are described.

Wright, C. W. and Coke, M. M. 1975. The artificial propagation of *Barbus natalensis*. 2. Hatching and early development. *Lammergeyer* **22:** 42–48.

This paper includes a brief descriptive account of several egg and larval stages of *Barbus natalensis*, no drawings accompanied the text. Development was followed for 68 days when excessive siltation suffocated the larval fish. Important behavioural aspects are noted, such as floating after the swim-bladder had inflated and burying themselves in the gravel substratum.

BAGRIDAE

Hirigoyen, J. P. and Petel, C. 1979. Nouvelles données sur la croissance en étang du poisson Bagridae *Auchenoglanis occidentalis* Valenciennes, 1840. *Not. Doc. Pêches Piscic. C.T.F. Nogent sur Marne* **18:** 20–26.

The larvae of *Auchenoglanis occidentalis* from the Bandama River (Ivory Coast) are briefly described. This paper is not illustrated.

Ikusemiju, K. 1976. Distribution, reproduction and growth of the catfish *Chrysichthys walkeri* (Günther) in the Lekki Lagoon, Nigeria. *J. Fish Biol.* **8**(6): 453–458.

Laboratory incubated eggs of *Chrysichthys walkeri* (= probably *C. auratus*) from Nigeria, hatched after three days, with the yolk sac being completely absorbed on the seventh day. The first day larva are about 8,6 mm TL. No other data on early ontogeny.

Pham, A. and Hirigoyen, J. P. 1979. Données préliminaires sur la reproduction provoquée de *Chrysichthys walkeri* Günther, 1899 (Poissons; Bagridae). *Not. Doc. Pêches Piscic C.T.F. Nogentsur Marne* **18:** 10–19, 6 figs.

The first results of induced spawning of *Chrysichthys walkeri* (= *C. maurus*) from Ivory Coast are discussed. Larval development is briefly described for the first eight days. Photographs of the eggs, the 18 hour old larvae and the 24 hour old larvae are included.

CLARIIDAE

Aboul-Ela, I. 1973. The embryonic and larval development of the Nile catfish, *Clarias lazera* Cuv. et Val.. *Proc. Seventh Arab. Sci. Cong., Cairo, Egypt.*

Not seen.

Bowmaker, A. P. M. 1973. *An hydrobiological study of the Mwenda River and its mouth, Lake Kariba.* Unpubl. Ph.D. thesis, Univ. of Witwatersrand.

The development of wild collected eggs and larvae of *Heterobranchus longifilis?* was followed. Earliest stage described is late gastrula. Illustrations of late gastrula and 5,3, 7,4, 7,6 and 8,4 mm TL larvae are included, with a brief description.

Bruton, M. N. 1979. The breeding biology and early development of *Clarias gariepinus* (Pisces; Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias* (*Clarias*). *Trans. zool. Soc. Lond.* **35:** 1–45, 10 figs.

As per title on *Clarias gariepinus* from Lake Sibaya, South Africa. This paper includes detailed descriptions and camera lucida drawings of the fertilized ova, the 33, 44, 56, 66 and 80 hour larvae, the ten and fourteen day fingerlings.

De kimpe, P. and Micha, J. C. 1974. First guidelines for the culture of *Clarias lazera* in Central Africa. *Aquaculture* **4:** 227–248, 13 figs.

Brief descriptions illustrated with photographs of larvae (24 hours/ 3 days/ 5 days after hatching) obtained through induced spawning of *Clarias lazera* (= *C. gariepinus*) from Central African Republic.

Greenwood, P. H. 1955. Reproduction in the catfish, *Clarias mossambicus* Peters. *Nature, Lond.*, **176:** 516–518, 1 fig.

This paper includes the first brief description of the eggs, embryos and larvae (up to one week) of *Clarias mossambicus* (= *C. gariepinus*) from Lake Victoria.

Greenwood, P. H. 1957. The reproduction of *Clarias mossambicus* Peters in Lake Victoria. *Publs Cons. scient. Afr. S. Sahara* **25:** 77–78.

Newly hatched larvae (3,5–4,0 mm TL) and 10,0 to 12,0 mm larvae of *Clarias mossambicus* (= *C. gariepinus*) from Lake Victoria are briefly described.

Hogendoorn, H. 1980. Reproduction et alevinage controlés du poisson—chat africain *Clarias lazera* (C. & V.). *Not. Doc. Pêches Piscic. C.T.F. Nogent sur Marne* **20:** 1–10.

The eggs, free embryo and larvae after resorption of the yolk sac of *Clarias lazera* (= *C. gariepinus*) are briefly described. The eggs were obtained from fish artificially induced to spawn.

Holl, E. A. 1968. Notes of spawning behaviour of barbel *Clarias gariepinus* Burchell in Rhodesia. *Zool. afr.* **3**(2): 185–188.

A very brief description is given of the eggs, the newly hatched free embryos (3,5–4,0 mm TL) and the seven day old larvae (7,0–9,0 mm TL) of *Clarias gariepinus* in Zimbabwe.

Janssen, J. 1985. *Elevage du poisson—chat africain Clarias lazera (Cuv. & Val., 1840) en République Centrafricaine*. II. Alevinage en écloserie. FAO, Proj. GCP/CAF/007/NET, Doc. Techn. Nr. 21, 31pp.

The early development (egg, hatching, 12h, 24h, 36h, 48h, 6 days, 9–12 days) of *Clarias lazera* (= *C. gariepinus*) from Central African Republic are described and illustrated.

Jocque, R. 1975. Sur quelques essais de reproduction induite chez *Clarias lazera* et *Clarias senegalensis*. *PNUD/AVB/FAO-IVC* 526 Rapp. Techn. **43:** 17, 3 figs.

Clarias lazera (= *C. gariepinus*) and *C. senegalensis* (= *C. anguillaris*) from Lake Kossou, Ivory Coast, were artificially induced to breed. Development of eggs and larvae is briefly described. The eggs of *C. senegalensis* (= *C. anguillaris*) are illustrated (camera lucida drawing).

Pham, A. 1975. Données sur la production en masse d'alevins de *Clarias lazera* Val. (Pisces; Clariidae). *Annls. Univ. Abidjan*, (E) **8**(1): 139–145.

Clarias lazera (= *C. gariepinus*) from Lake Kossou (Ivory Coast) were artificially induced to breed. The first fifteen days in the development of the larvae are very briefly discussed.

Weeks, D. 1984. Embryological and larval development of catfish *Clarias gariepinus* (Burchell) (Pisces: Clariidae). Unpubl. BSc. project, Rhodes Univ. 20pp., 7 figs.

Clarias gariepinus were artificially induced to spawn. Development was followed from first cleavage to metalarval phase. Early cleavage, blastula, gastrula, embryonic and protolarval, mesolarval and metalarval stages are illustrated.

Zaki, M. I. and Abdula, A 1983. The reproduction and development of *Clarias gariepinus* (Clariidae) from Lake Manzala (Egypt). *J. Ichthyol.* **23**(6): 48–58, 6 figs.

Detailed data are given on the structure of the eggs, nature of spawning, embryonic and larval periods of development of *Clarias gariepinus* in Lake Manzala, Egypt. Development is followed from the mature egg before fertilization, up to the 39 day old juvenile. Illustrations of 19 stages of embryonic and 13 larval stages are included.

MOCHOKIDAE

Van Der Waal, B. C. W. 1986. Note on artificial fertilization and early development of *Synodontis nigromaculatus* (Pisces: Mochokidae). *S. Afr. J. Zool.* **21**(3): 269–271.

Eggs were obtained from a wild gravid female of *Synodontis nigromaculatus* in the Okavango Swamps. Development was followed from activation to the mesolarval stage, 10 days after fertilization. Photographs of several stages, 7h, 10h, 22h embryo, newly hatched prolarva (35h), 54h prolarvae and 9,5 day old mesolarva are included. The developmental series is housed at the Albany Museum, Grahamstown, South Africa, (AMG/P 11189).

CYPRINODONTIDAE

Avni, A. A. and Soin, S. G. 1974a. Adaptive characteristics of the embryogeny of *Nothobranchius guentheri* in connection with existence in temporary tropical habitat. *J. Ichthyol.* **14**(5): 735–746, figs.

Nothobranchius guentheri from East African Coasts and Zanzibar are studied. Detailed descriptions and drawings are included from the egg, soon after fertilization, up to the larval stage, 3–4 days after hatching.

Avni, A. A. and Soin, S. G. 1974b. Adaptive peculiarities of *Nothobranchius guentheri* (Pfeffer) embryogenesis in connection with life in periodically drying out tropical waters. *Vopr. ichtiologii* **14:** 846–858 (in Russian).

Not seen. after BALON 1977 and 1985. See AVNI and SOIN 1974a.

Kroll, W. 1984. Morphological and behavioural embryology and spontaneous diapause in the African killifish *Aphyosemion gardneri/Austrofundulus myersi* developmental arrest hatching adaptation. *Environ. Biol. Fishes* **11**(1): 21–28.

Laboratory stock of *Aphyosemion gardneri* were bred in aquaria and the development of the resulting eggs was followed. A brief account of the chronology of developmental events is given from early cleavage to hatching. Eight photomicrographs depict early cleavage, epiboly completion, organogenesis and a newly hatched free embryo. Diapause is discussed at certain developmental points for annual killifishes.

Peters, N. 1963. Embryonale Anpassungen oviparer Zahnkarpfen aus periodisch austrockrenden Gewässer. *Int. Revue ges. Hydrobiol. Hydrogr.* **48**(2): 257–331.

Not seen.

Rasmussen, E. 1948. Spawning and early development of *Epiplatys chaperi*. *Aquar. J.* **19**(5): 23–25.

Not seen.

Terceira, A. C. 1977. Comparative observations on the early embryology of *Nothobranchius korthausae* and *Epiplatys sheljuzhkoi*. With special reference to predicting the onset of diapause. I. *J. Amer. Killifish Ass.* **10**(10): 242–251.

Not seen.

Terceira, A. C. 1982. Observations comparatives sur le développement embryologique primaire de *Nothobranchius korthausae* et *Epiplatys sheljushkoi*. *Killi Revue* **6:** 12–24 (French translation), figs.

The eggs and the embryonic development of two Cyprinodontidae, *Nothobranchius korthausae* from Sierra Leone and *Epiplatys sheljushkoi* from about 75 miles from Dar-es-Salaam, Tanzania were studied using compound (for the eggs) and dissecting (for the embryos) microscopes. The development was followed for about ten days. Camera lucida drawings of the eggs and the embryo are included.

Wourms, J. P. 1965. Comparative observations on the early embryology of *Nothobranchius taeniopygus* (Hilgendorf) and *Aplocheilichthys pumilus* (Boulenger) with special reference to the problems of naturally occurring diapause in teleost fishes. *Rep. E. Afr. Freshw. Fish. Res. Org.* (1964): 68–73.

The developmental pattern of *Nothobranchius taeniopygus* from the Sio River, Kenya and *Aplocheilichthys pumilus* from Lake Victoria are briefly described. The development of the eggs was followed, using both dissecting and compound microscopes, for about 204 hours and 112 hours respectively. No drawings are included.

Wourms, J. P. 1969. Comparative observations on the early embryology of *Nothobranchius taeniopygus* (Hilgendorf) and *Aplocheilichthys pumilus* (Blgr.) with special reference to the problem of naturally occurring embryonic diapause in teleost fishes. *Rep. E. Afr. Freshwat. Fish. Res. Org.* (1968): 68–73.

Not seen.

Wourms, J. P. 1972. The developmental biology of annual fishes. II. Naturally occurring dispersion and reaggregation of blastomeres during development of annual fish egg. *J. exp. Zool.* **182:** 169–200.

The dispersion and subsequent reaggregation of pre-embryonic blastomeres is discussed. Several African annual fishes are compared to the development of *Austrofundulus myersi*. These include *Nothobranchius guentheri, N. palmquistii, Aphyosemion arnoldi, A. calliurum, A. fallax, A. nigerianum, A. walkeri, A. sjoestedti* and *Roloffia occidentalis* (= *A. occidentale*).

Photomicrographs of the early and late blastula and of Epon sections to show dispersed and reaggregated state of *Austrofundulus myersi* eggs are included.

CENTROPOMIDAE

Hopson, A. J. 1969. A description of the pelagic embryos and larval stages of *Lates niloticus* (L.) (Pisces: Centropomidae) from Lake Chad, with a review of early development in lower percoid fishes. *Zool. J. Linn. Soc.* **48**(1): 117–134, 8 figs.

Eggs and larval development of *Lates niloticus* from Lake Chad are described in detail and illustrated from the advanced embryo up to the juvenile period (13,0 mm TL). Twelve arbitrary stages are defined to illustrate larval development.

CICHLIDAE

Abu Gideiri, Y. B. 1969. The development of behaviour in *Tilapia nilotica* L.. *Behaviour* **34:** 17–28, 4 figs.

Development and movements in embryos of *Tilapia nilotica* (= *Oreochromis niloticus*) were observed through the egg membranes, using a binocular microscope, at regular intervals until hatching. Some embryos were fixed for histological sections, stained by silver impregnation and drawn with the aid of a camera lucida.

Arnold, M., Kriesten, K. and Peters, H. M. 1968. Die Haftorgane von *Tilapia*-Larven (Cichlidae, Teleostei) Histochemische und elektronenmikroskopische Untersuchungen. *Z. Zellforsch. mikrosk. Anat.* **91:** 248–260.

This paper includes histochemical and electron microscopical investigations on cement glands of larval *Tilapia mariae* and *Tilapia nilotica* (= *Oreochromis niloticus*), three to six day old larvae.

Assheton, R. 1907. Report upon sundry Teleostean eggs and larvae from the Gambia River. In: Kerr, G. *ed. Budgett Memorial volume—1907.* Cambridge: Univ. Press, pp. 433–442, 6 figs.

Descriptions illustrated with drawings of sagittal sections of early cleavage egg and embryonic stages in the development of *Hyperopisus bebe* (= *Tilapia guineensis*) from the Gambia River. Specimens collected every few hours for 3 days and once a day for 3 additional days by Budgett, Assheton notes stage too early for positive identification. Included are descriptions of early cleavage stage of 114 blastomeres, late stage of cleavage, stage with subgerminal cavity, stage after envelopment of the yolk mass by the blastoderm.

Balon, E. K. 1977. Early ontogeny of *Labeotropheus* Ahl 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *Environ. Biol. Fishes.* **2**(2): 147–176, 25 figs.

A detailed study of the ontogeny of *Labeotropheus sp.* (= *Labeotropheus trewavasae* or *L. fuelleborni*) from Lake Malawi, based on observations *in vivo* and using alizarin stained specimens. The form and the size of the eggs at several stages of development are discussed and drawn. Photographs of stages in the cleavage, embryonic and eleutheroembryonic (= free embryo) phases are included; furthermore drawings of the initial stages of epiboly, the first stages in embryonic phase, the beginning of heart and vessel formation, of the stage shortly before and shortly after hatching, of the eleutheroembryos and of the end of endogenous nutrition. Eleutheroembryo develops without metamorphic larval stages directly into a juvenile.

Balon, E. K. 1981. Saltatory processes and altricial to precocial forms in the ontogeny of fishes. *Am. zool.* **21:** 573–593, figs.

This paper includes discussions and drawings of an eleutheroembryo of the mouthbrooding cichlid *Labeotropheus* from Lake Malawi (see Balon 1977).

Balon, E. K. 1985. Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and

development. In: Balon, E. K. *ed. Early life histories of fishes*. Dordrecht: Junk, pp. 207–236.

Duplicate of Balon (1977), see above.

Breder, C. M. Jr. 1943. The eggs of *Bathygobius soporator* (C.V.) with a discussion of the other non-spherical teleost eggs. *Bull. Bingham oceanogr. Coll.* **8**(3): 1–49, 16 figs.

This paper includes data and drawings of the eggs, of amongst others, *Tilapia macrocephala* (= *Sarotherodon melanotheron*).

Budgett, J. S. 1901a. On the breeding habits of some West African fishes, with an account of the external features in the development of *Protopterus annectens, and a description of the larva of Polypterus lapradei. Trans. zool. Soc. Lond* **16**(2): 115–136, 5 figs, 2 pls. (Also in: Kerr, G. *ed. Budgett Memorial Volume—1907*. Cambridge: Univ. Press, pp. 119–136, 2 pls.)

The eggs and larvae of *Hyperopisus bebe* (= *Tilapia guineensis*) from the Gambia River are briefly described. Habitat drawings of eggs and larvae, and drawing of cement glands on larvae are included.

Budgett, J. S. 1901b. The habits and development of some West African fishes. *Proc. Camb. phil. Soc.* **11:** 102–104. (Also in: Kerr, G. *ed. Budgett Memorial Volume—1907*. Cambridge: Univ. Press, pp. 141–142.)

The eggs and larvae of *Hyperopisus bebe* (= *Tilapia guineensis*) from the Gambia River are briefly described.

Daget, J. 1952. Observations sur une ponte de *Tilapia zillii* (Gervais), poisson de la famille des Cichlides. *Ann. Mag. nat. Hist.* (12)**5**(51): 309–310.

The eggs and larvae of *Tilapia zillii* from Diafarabe, Central Niger system are briefly described.

Donnelly, B. G. and Caulton, M. S. 1973. A note on the breeding behaviour and larval development of *Tilapia sparrmanii* Smith (Pisces—Cichlidae). Unpubl. report, Rhodes Univ. 16pp.

The developmental sequence after hatching was divided into eight stages, characterized by specific morphological or behavioural characters, which are described. Eleven photomicrographs of the egg and early larval to juvenile stages are included.

El Zarka, S. and Ezzat, A. 1972. Embryology and larval development of *Tilapia galilaea* Art. *C.I.E.S.N.Rapp. Proc. Verb. Réun.* Monaco 1972, **20**(4): 499–501, pl.

The embryology and larval development of *Tilapia galilaea* (= *Sarotherodon galilaeus*) from the Nile are briefly described.

Fishelson, L. 1966. *Comparative investigations of the development of some fish species of the genus* Tilapia *(Cichlidae)*. Unpubl. thesis, Hebrew Univ.

Not seen.

FISHELSON, L. 1966. Untersuchungen zur vergleichenden Entwicklungsgeschichte der Gattung *Tilapia* (Cichlidae, Teleostei). *Zool. Jb. (Anat.)* **83:** 571–656.

The early development in *Tilapia tholloni* from the 22 hour old embryo to the 10 day old larva is described with drawings and photomicrographs of the 2, 3, 4, 5 and 6 day stages. Comparison is made to the development of *T. macrocephala* (= *Sarotherodon melanotheron*), *T. nilotica* (= *Oreochromis niloticus*).

FRANCOIS, Y. 1958. Recherches sur l'anatomie et le développement de la nageoire dorsale des Téléostéens. *Archs Zool. exp. gén.* **97:** 1–108.

The dorsal fin development in, amongst others, *Tilapia monodi* (= *Oreochromis aureus*) is discussed. Drawings of transversal section of the dorsal fin region in 5,5 mm and 7 mm larvae are included.

IMAM, A. E. AND HASHEM, M. T. 1960. Notes on the breeding behaviour, embryonic and larval development of *Tilapia zillii* Gervais. *Notes & Mem. Hydrobiol. Fish. Dir., Cairo* **51:** 1–17, 7 figs.

The embryonic and larval development of *Tilapia zillii* from Lake Manzala (Egypt) are discussed and stages in development are drawn, from the fertilized (1,4–1,6 mm) eggs up to the one month old fry (16 mm). The external morphology of the different stages is described.

ISMAIL, M. H. 1984. The postembryonic development of the chondrocranium in the Nile fish *Sarotherodon galilaeus* Linnaeus (Teleostei; Cichlidae). 2. The postbuccal stages. *Arab. Gulf J. Sci. Res.* **2**(1): 221–238.

The development of the chondrocranium of two postbuccal stages of *Sarotherodon galilaeus* (9 mm and 12 mm TL; 11/14 days after fertilization) is described and compared to that of other bony fishes.

JONES, A. J. 1972. The early development of substrate-brooding cichlids (Teleostei: Cichlidae) with a discussion of a new system of staging. *J. Morph.* **136:** 255–272.

The gametic and the embryonic periods of *Hemichromis bimaculatus* and four South American cichlids are described and illustrated with camera lucida drawings.

JURGENS, W. 1910. Ueber die Larven von *Hyperopisus bebe* Lac. *Bl. Aquar.-u. Terrarienk.* **21:** 163–164.

This paper is based on the work of Budgett (1900) with descriptions and drawings of the larvae of *Hyperopisus bebe* (= *Tilapia guineensis*).

LANZING, W. J. R. 1976. A temporary respiratory organ in the tail of *Tilapia mossambicus* fry. *Copeia 1976: 800–802.*

The temporary respiratory organ which occurs during the development of *Tilapia mossambica* (= *Oreochromis mossambicus*) is described. Camera lucida drawings of the 5 day old larvae are included.

McEwan, R. S. 1930. The early development of *Hemichromis bimaculatus*, with special reference to factors determining the embryonic axis. *J. Morph.* **49:** 579–619.

The early development in *Hemichromis bimaculatus* is described and drawn, in particular from the fertilized egg up to 22 hours after spawning.

McEwan, R. S. 1940. The early development of the swimbladder and certain adjacent parts in *Hemichromis bimaculatus*. *J. Morph.* **67:** 1–40.

Not seen.

Peters, H. M. 1965. Ueber larvale Haftorgane bei *Tilapia* (Cichlidae, Teleostei) und ihre Rückbildung in der Evolution. *Zool. Jb. (Zool. und Physiol.)* **71:** 287–300, 8 figs.

The cement glands in larvae of substrate breeding *Tilapia* (*T. tholloni; T. mariae*) are described and illustrated (camera lucida drawings) and compared with the rudimentary cement glands in larvae of mouth breeding *Tilapia* (*Tilapia macrocephala* = *Sarotherondon melanotheron; Tilapia mossambicus* = *Oreochromis mossambicus; Tilapia nilotica* = *Oreochromis niloticus*).

Peters, H. M. and Berns, S. 1982a. Die Maulbrutpflege der Cichliden. Untersuchungen zur Evolution eines Verhaltensmusters. *J. zool. Syst. Evolut.-forsch.* **20:** 18–52.

Not seen.

Peters, H. M. and Berns, S. 1982b. Larvophile und ovophile Maulbrüter. *Tatsachen und Informationen aus der Aquaristik* **58:** 19–22, 5 figs. (1 col.).

Not seen.

Rifaat, A., El-Din El-Zarka, S. and Ezzat, A. 1964. Tilapia fisheries investigation in Egyptian lakes. 4. The embryology and larval development of *Tilapia zillii* (Gerv.) from Lake Mariut, Egypt. *Notes & Mem. Alexandria Inst. Hydrobiol.* **72:** 1–9, 18 figs.

The embryonic and larval development of *Tilapia zillii* from Lake Mariut, Egypt are discussed from the fertilized ovum (1,6 mm) up to stage 21 (the 60 days post larva-13 mm). The stages examined are illustrated with photographs and camera lucida drawings.

Shaw, E. S. 1956. Two weeks in father's mouth. *Nat. Hist., N.Y.* : 152–153, figs.

Photomicrographs and descriptions of various stages in the development of *Tilapia macrocephala* (= *Sarotherodon melanotheron*) from the zero hour egg to the fifteen day old larvae are included (see also Shaw and Aronson 1954).

Shaw, E. S. and Aronson, I. R. 1954. Oral incubation in *Tilapia macrocephala*. *Bull. Am. Mus. nat. Hist.* **103:** 375–416, 4 figs, 13 pls.

Detailed descriptions and photomicrographs of the development in *Tilapia macrocephala* (= *Sarotherodon melanotheron*) based on examinations in the living state, from the unfertilized ovum (2,0–3,5 mm) up to the hatching stage (stage 24) (5,3 mm). Photomicrographs were made

of several serial sections, stained with Harris' haematoxylin and eosin or a modification of the Masson trichrome stain.

Welcomme, R. L. 1967. The relationship between fecundity and fertility in the mouthbrooding cichlid fish *Tilapia leucosticta*. *J. Zool.* **151:** 453–468, 6 figs.

The development, from egg up to the 11,0 mm larvae (17 days old) of *Tilapia leucosticta* (= *Oreochromis leucostictus*) reared in an artificial mouth is discussed using tables and drawings.

Welcomme, R. L. 1969. The biology and ecology of the fishes of a small tropical stream. *J. Zool.* **158:** 485–529, 18 figs.

An account is given of the development of the mouthbrooder *Hemihaplochromis multicolor* (= *Pseudocrenilabrus multicolor*) with tables and drawings of the larvae, five, six, eight, ten and fourteen days after fertilization.

GOBIIDAE

Breder, C. M. Jr. 1943. The eggs of *Bathygobius soporator* (C.V.) with a discussion of other non-spherical teleost eggs. *Bull. Bingham oceanogr. Coll.* **8**(3): 1–49, 16 figs.

This paper includes data on and drawings of eggs of *Gobius niger*.

Tavolga, W. N. 1950. Development of the gobiid fish *Bathygobius soporator*. *J. Morph.* **87**(3): 467–492.

Not seen.

ANABANTIDAE

Barnard, K. H. 1943. Revision of the indigenous freshwater fishes of the S.W.Cape region. *Ann. S. Afr. Mus.* **36**(2):101–262.

A juvenile (= larval) *Sandelia capensis* is briefly described. Two larval fish are illustrated.

Berns, S. and Peters, H. M. 1969. The reproductive behaviour of *Ctenopoma muriei* and *Ctenopoma damasi* (Anabantidae). *Rep. E. Afr. Freshwat. Fish. Res. Org.* (1968) : 44–49.

The developing eggs of *C. muriei* and *C. damasi* are briefly described. The egg, newly hatched larva and a four day old larva are illustrated.

Morik, D. 1977. *Vergleichende Untersuchungen zur Ethologie zweier Labyrinthfischarten,* Ctenopoma muriei *(Boulenger, 1906) und* Ctenopoma damasi *(Poll, 1939), Anabantoidea, Pisces)*. Unpubl. Ph.D. thesis. Univ. of Tübingen.

The cleavage egg, embryonic and free embryo phases are illustrated and photomicrographs of the free embryo, larval and juvenile fish are included. Includes a brief description of development including an histological study of swimbladder development.

Table 1.

Summary of number of papers dealing with the early development of African freshwater fishes.

FAMILY	No. of Papers	No. of Species	No. of species illustrated	
			Drawings	Photographs
PROTOPTERIDAE	12	2	2	—
POLYPTERIDAE	17	3	1	1
CLUPEIDAE	13	8	8	1
OSTEOGLOSSIDAE	7	1	1	—
NOTOPTERIDAE	1	1	—	—
MORMYRIDAE	5	3	2	1
GYMNARCHIDAE	9	1	1	1
HEPSETIDAE	5	1	1	—
CHARACIDAE	6	4	2	1
CYPRINIDAE	15	16	13	1
BAGRIDAE	3	3	—	1
CLARIIDAE	13	3	4	1
MOCHOKIDAE	1	1	—	1
CYPRINODONTIDAE	10	7	3	1
CENTROPOMIDAE	1	1	1	—
CICHLIDAE	30	14	12	5
GOBIIDAE	2	2	1	—
ANABANTIDAE	3	2	2	2
TOTALS	153	73	54	17

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> Jubb, R. A. 1967. *Freshwater fishes of southern Africa.* Cape Town: Balkema.

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A contribution to the knowledge of the ethology of the genera *Parachilus* Giordani Soika and *Paravespa* Radoszkowski (Hymenoptera: Eumenidae) in southern Africa

by

F. W. GESS and S. K. GESS

(Albany Museum, Grahamstown)

ABSTRACT

Ethological accounts are given for *Parachilus capensis* (Saussure), *Parachilus major* (Saussure) and *Paravespa (Gestrodynerus) mima* Giordani Soika. The two species of *Parachilus*, like *Parachilus insignis* (Saussure), divide their cells into an egg compartment and one or more pantry compartments. The cells of *Paravespa (Gestrodynerus) mima* Giordani Soika are not divided. Nest turrets of two distinct architectural forms are recorded for *P. (G.) mima*.

INTRODUCTION

The genus *Parachilus* Giordani Soika (1960) is restricted in its distribution to the Afrotropical Region and includes ten species, six of which occur in southern Africa (Giordani Soika, 1960 and 1985). The account of the nesting of *Parachilus insignis* (Saussure) (Gess and Gess, 1976) is to date the only account of nesting for this genus. The surprising discovery that *P. insignis* divides its cells into two compartments, an egg compartment and a pantry compartment led the authors to seek for nests of other species of the genus *Parachilus* and of closely related genera in order to establish whether this behaviour is restricted to *P. insignis* or to the genus *Parachilus*, or is of wider occurrence. Two nests of *Parachilus capensis* (Saussure) were discovered in the summer of 1976/77 but no further nests of this species or of any other species of *Parachilus* were found until seven nests of *Parachilus major* (Saussure) were discovered in October 1987.

The genus *Paravespa* Radoszowski is composed of two sub-genera, *Paravespa* Radoszowski which is restricted to Palaearctic Asia, and *Gestrodynerus* Giordani Soika which is restricted to the Afrotropical Region (Giordani Soika, 1960). Eleven species of *Gestrodynerus* have been described and of these four have been recorded from southern Africa (Giordani Soika, 1960 and 1985). A relatively large number of nests of *Paravespa (Gestrodynerus) mima* Giordani Soika was located during December 1987 and seventeen of these were investigated. As *Paravespa* is related to *Parachilus* (Carpenter, pers. comm.) a comparison between the nesting of representatives of these two genera is of interest.

ETHOLOGICAL ACCOUNTS

Parachilus capensis (Saussure)

Geographical distribution

Parachilus capensis is known from the Cape Province from: Somerset East, Klaver, Kamieskroon, Oliphants River between Citrusdal and Clanwilliam (Giordani Soika, 1960); Somerset East, Matjesfontein, Ceres and Camps Bay (British Museum (N.H.) collection); and the farms Thursford, Hilton, Lynton, Vlakwater and Vaal Vlei (Mosslands) in the Grahamstown district, Alicedale (New Years Dam), and the Ouberg Pass (27 km NE of Montagu) (Albany Museum collection).

Description of the nesting area

A nesting area of *Parachilus capensis* was located in the valley of the New Years River on the farm Hilton, 18 km WNW of Grahamstown (33° 19′ S, 26° 32′ E) in the Eastern Cape Province. The farm receives an annual rainfall of 356 mm. The vegetation of the area as a whole is Acocks' Veld Type 37, False Karroid Broken Veld (Acocks, 1953 and 1975). That in the immediate vicinity of the nesting sites is more specifically dwarf scrub. *Pentzia incana* (Th.) O.Ktze and *Chrysocoma tenuifolia* Berg. (both Compositae) predominate. The nests were excavated in fine grained non-friable clayey soil in a bare area below a water furrow (Gess and Gess, 1976: Plate 2). (For a full description of the area as a whole see Gess, 1981).

Identification of the prey

A total of 12 prey caterpillars of *Parachilus capensis* was obtained, 11 from a single sealed cell and 1 from a female which was transporting it to her nest. Two species of Psychidae (bagworms) were represented. On comparison these were found to be indistinguishable from the two species recorded as utilized by *Parachilus insignis* (Gess and Gess, 1976). Nine of the caterpillars were of the species with the pale ochreous, brown-spotted head and three were of the species with the rufous head. All bore sting lesions anterior to the legs on the prothorax and metathorax and three in addition bore sting lesions anterior to the legs on the mesothorax. No sting lesions were found on the abdomen.

Provenance of prey

The species with the pale ochreous, brown-spotted head has been found feeding on *Pentzia incana* and that with the rufous head on a yellow daisy-flower (? *Gazania* sp.) (Compositae) at Hilton (Gess and Gess, 1976).

Description of the nest, egg and distribution of the provision

The nest of *Parachilus capensis* consists of a subterranean burrow surmounted by a mud turret (Fig. 1). Only two nests have been found (Nest 1 on 10.xi.1976 and Nest 2 on 3.i.1977). The turrets of these two nests were constructed from loosely cemented mud pellets with no attempt having been made at smoothing. The turrets were funnel-shaped. The inner diameter at the base of each turret was equal to that of the opening of the respective main shaft, 6 mm in Nest 1 and 7 mm in Nest 2, and that at the lip was *c* 15 mm and 20 mm respectively.

Nest 1 consisted of a short vertical shaft leading to two curved branches which descended to a depth of 36 mm. One of these branches was sealed off from the main shaft by a mud plug. The entire sealed off portion, 31 mm in length, constituted a cell divided by three mud plates

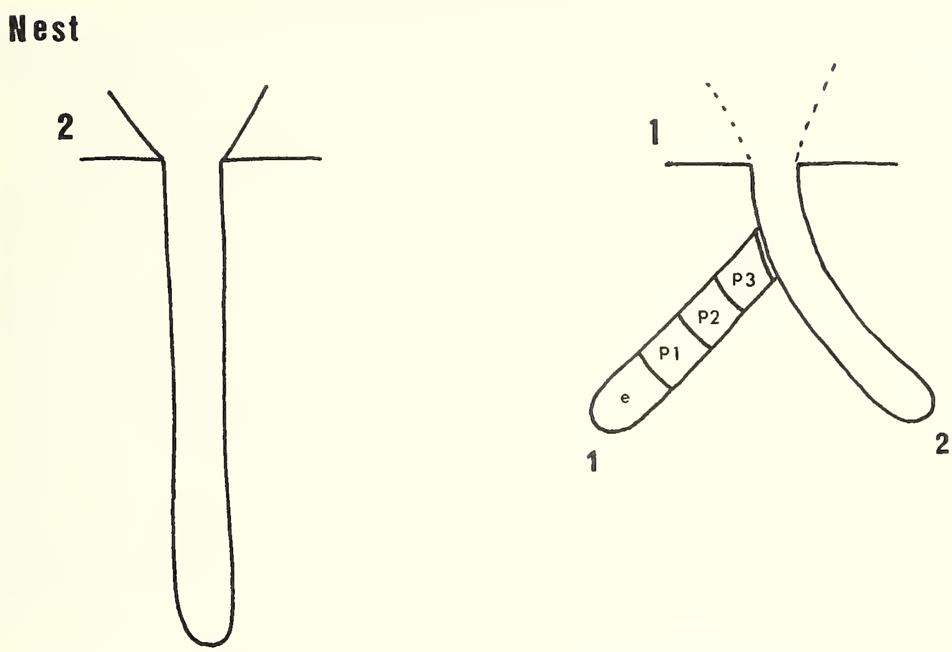

Fig. 1. Vertical plans of turrets and underground workings of nests of *Parachilus capensis* (Saussure) (× 1). e–egg compartment; p–pantry compartment.

into four compartments. The innermost compartment, the egg compartment, contained an egg and two caterpillars. The egg was yellow, slightly curved, 2,83 mm long and 0,92 mm wide at mid-length. It was attached to the cell wall by a filament. The second, third and fourth compartments, all pantry compartments, contained three, four and two caterpillars respectively (see Table 1).

Table 1.

Analysis of the provision from the closed cell of Nest 1 of *Parachilus capensis* (Saussure).

Part of nest	No. of prey constituting provision	Mass of provision mg
closed egg compartment	2	123
closed pantry compartment 1	3	200
closed pantry compartment 2	4	208
closed pantry compartment 3	2	186
combined pantry compartments 1 + 2 + 3	9	594

The other branch of the burrow was clearly the second to be excavated. Though empty it was undoubtedly a second cell as the nest builder was captured bringing in prey.

The discarded pellets, 5 mm in diameter, had been dropped in a pellet dropping area 60 mm in diameter and 300 mm from the nest entrance.

Nest 2 had clearly been usurped by a sphecid wasp as it contained 2 grasshoppers and had been filled in with earth and debris.

Reaction to rain damage

The turret of Nest 1 which was still being provisioned was destroyed by rain during the period that the nest was under observation. The wasp made no attempt to rebuild it.

Parachilus major (Saussure)

Geographical distribution

Parachilus major is known from the southern and western Cape Province from: Matjesfontein and Willowmore (Giordani Soika, 1960); Matjesfontein and Worcester (British Museum (N.H.) collection); Augusfontein (Calvinia), Zebra (Oudtshoorn), Venterstad Region, Swart Doringrivier (Namaqualand) and Hester Malan Nature Reserve (Springbok, Namaqualand) (Albany Museum collection).

Description of the nesting area

A nesting area of *Parachilus major* was located in the Hester Malan Nature Reserve. This reserve lies 12 km east of Springbok in the Carolusberg, in the region of Namaqualand termed Namaqualand Klipkoppe which is characterized by rocky hills and Eindoorn granite domes and receives an annual rainfall of 100–200 mm. The area in which the nests of *P. major* were located was an east facing slope between the bed of the Droëdap River and the rocky hill tops. The vegetation of the reserve is classified Acocks' Veld Type 33, Namaqualand Broken Veld (Acocks, 1953 and 1975; and van Rooyen, Theron and Grobbelaar, 1979). That of the nesting area is characterized by dwarf shrubs. The dominant plants are Mesembryanthemaceae and perennial Compositae. The nests were sited in sloping ground in bare patches between plants (Fig. 2). The soil in which they had been excavated although coarse and sandy is non-friable and when moistened is malleable.

Water collection

Parachilus major, at the time of the investigation in the Hester Malan Nature Reserve, 15–21.x.1987, was collecting water for nest construction from a puddle, in a rut in the road, fed by a trickle seeping out from the bank above the road. In 1966 this species was collected when it was found in large numbers visiting residual saline pools in the bed of the Swart Doringrivier between Bitterfontein and Garies (F. W. Gess and W. H. R. Gess, 2–3.x.1966).

Identification of the prey

A total of 54 caterpillars was recovered from nine cells of *Parachilus major*. Two species of Psychidae (bagworms) were represented. On comparison these were found to be indistinguishable from the two species taken from the nests of *Parachilus insignis* and *Parachilus capensis* at Hilton. Fifty were of the species with the pale ochreous, brown-spotted head and four were of the species with the rufous head. The two species did not differ from each other in size and taken together both species ranged in length from 7,3–16,0 mm (average 11,5 mm, sample of 52). As a general rule each caterpillar exhibited at least one sting lesion on the underside of each thoracic segment, in all cases positioned anterior to the legs. The incidence of stings on the prothorax,

Fig. 2. Nesting area of *Parachilus major* (Saussure) in the Hester Malan Nature Reserve, 18.x.1987. The nesting sites were in bare patches. The water source was the puddle in road rut in foreground.

mesothorax and metathorax was 100%, 90% and 84% respectively. Some caterpillars also had sting lesions on the first or first and second abdominal segments. The incidence of stings on these two segments was 25% and 11% respectively. Whereas sting lesions on the abdomen were in some instances present in specimens lacking lesions on the mesothorax or metathorax, in others they were additional to those on the three thoracic segments.

Prey provenance

It seems likely that in the Hester Malan Nature Reserve the species with the pale ochreous, brown-spotted head feeds on the same plant as it does at Hilton, that is on *Pentzia incana*, which is present in the vicinity of the nesting sites of *Parachilus major*. The species with the rufous head, which feeds on yellow daisy-flowers at Hilton, presumably feeds on one or more of the daisy-flowered species which are not uncommon in the vicinity of the nesting sites of *P. major*.

Description of the nest

The nest of *Parachilus major* consists of a subterranean burrow surmounted by a mud turret (Fig. 3). The turret which is constructed from mud pellets is a vertical or sloping tube with the diameter at the base equal to that of the shaft and that at the distal opening the same or somewhat greater. The subterranean burrow consists of a short sloping main shaft terminating in a sub-vertical cell and additional sub-vertical to sloping cells terminating secondary shafts each nearer to the burrow entrance than that preceding it. The cell diameter is equal to or only slightly in excess of that of the shaft, the sides are parallel and the ends truncate. Each cell is divided into

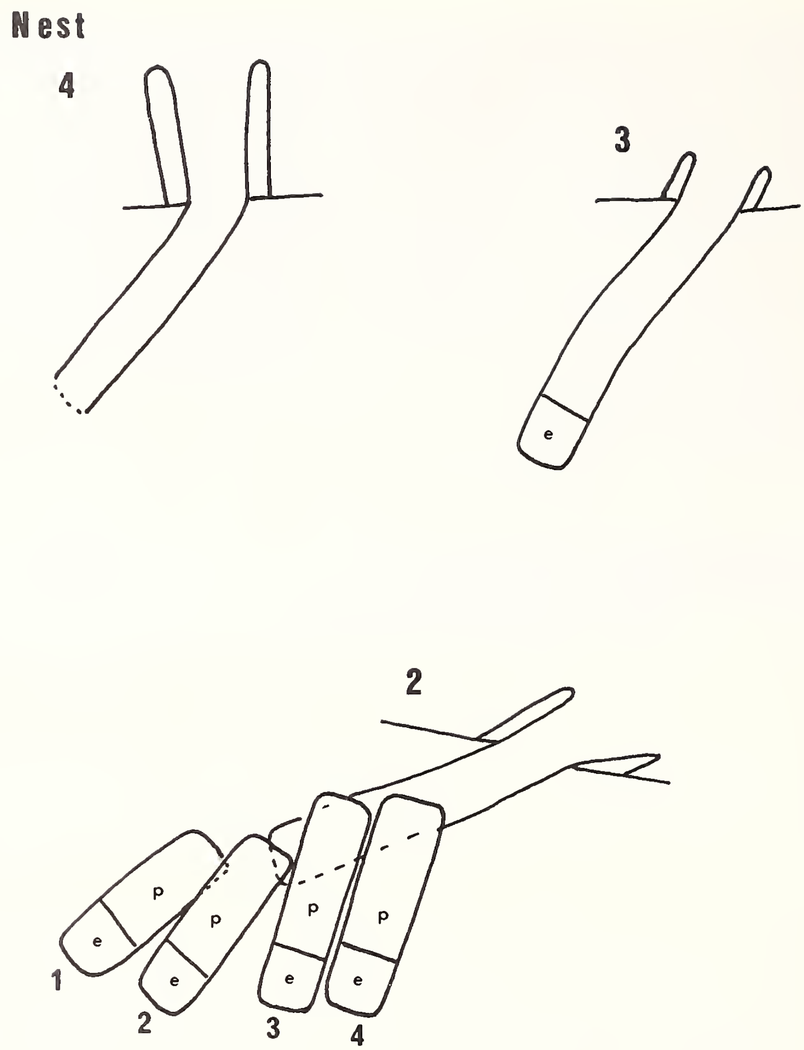

Fig. 3. Vertical plans of turrets and underground workings of nests of *Parachilus major* (Saussure) (× 1). e–egg compartment; p–pantry compartment.

two compartments, a lower egg compartment and an upper pantry compartment separated by a thin mud partition.

Method of construction of the nest, oviposition and provisioning

Water which is required for nest excavation is fetched in the crop from a nearby pool. A female whilst filling her crop stands on the mud at the edge of the water.

The turret is constructed early in nest excavation. Pellets are laid down around the shaft initial in such a way that the base of the turret is of the same diameter as that of the shaft, that is 7,0–8,0 mm (average 7,6 mm, sample of 5). Pellets are added in such a way that the final diameter is somewhat greater than the initial diameter. In the sample the difference ranged from 1 to 3,5 mm. The pellets used in turret construction are closely packed and no interstices are left open. Only the inside of the turret is smoothed. After turret construction is completed shaft excavation continues, further pellets from the excavation being discarded.

The main shaft, which initially slopes downwards at a constant angle, is terminated by a cell which is excavated at a much steeper angle. The diameter of the cell differs only marginally, 0,5 mm, if at all, from that of the shaft which gives rise to it. The inner end of the cell is truncate. The wasp clearly rotates in a constant direction whilst excavating as the end wall bears a noticably spiral pattern.

After a cell has been excavated oviposition takes place. An egg, bright yellow, only slightly curved, 3,5 mm from tip to tip and 1 mm wide at mid-length is attached to the cell wall by a filament 0,5 mm in length. Provisioning then takes place. A small number of prey is placed in the cell and a thin mud plate is then constructed completing the egg compartment. Hunting then continues and the rest of the provision is stored in the upper part of the cell, the pantry compartment (Table 2).

Table 2.

Analysis of the provision from eight cells of *Parachilus major* (Saussure).

Part of nest	Size of sample	No. of prey constituting provision (range)	No. of prey constituting provision (average)
Closed egg compartment	8	1–2	1,8
Closed pantry compartment	6	3–9	6,7
Complete cells	6	5–11	8,7

Provisioning having been completed the cell is sealed with a mud plug and firmly packed earth. Successive cells terminate successive steeply sloping secondary shafts each one being nearer to the burrow entrance than that preceding it so that the cells lie close together and more or less parallel to each other.

The total length of a cell, that is egg compartment plus pantry compartment, ranged from 21–30 mm. The eight egg compartments measured were all 8 mm in length. The variation in cell length is therefore due to a variation in the length of the pantry compartment. Of the eight cells for which the diameter was measured all but one had a diameter of 7,5 mm.

Seven nests were located and excavated. Two of these which lacked turrets were old nests from which wasps had emerged. One was one-celled and the other three-celled. The remaining five nests were surmounted by turrets. Two had not yet reached the stage of cell excavation, one was one-celled and two were four-celled. From such a small sample it is not possible to determine the maximum number of cells likely to be excavated. The excavation of each cell nearer to the nest opening than the one preceding it would, however, seem to preclude the

excavation of a large number of cells unless additional cells are excavated from other shafts lateral to the main shaft.

Paravespa (Gestrodynerus) mima Giordani Soika

Geographic distribution

Paravespa (Gestrodynerus) mima is known from the Cape Province from: Willowmore (Giordani Soika, 1960); Doornberghoek (Karoo Region), Port Alfred, Cradock, near Lake Mentz, Andries Vosloo Kudu Reserve, Bloutoring, the farms Frischgewaagd and Onverwacht (Oudtshoorn district) and Tierberg (Prince Albert district) (Albany Museum collection) and from the Orange Free State from: Chicago (Lindley district) (Albany Museum collection).

Description of the nesting area

Two nesting areas of *Paravespa (G.) mima* were located, one at Onverwacht, Oudtshoorn district and the other at Tierberg, Prince Albert district. That at Onverwacht (33° 37′ 35″S, 22° 14′ 18″E) which lies immediately inland of the Outeniqua Mountains receives an annual rainfall of 240 mm and that at Tierberg (33° 42′S, 22° 16′ 24″E) which lies inland of both the Outeniqua Mountains and the Swartberg receives only 170 mm. Both areas lie in Acocks' Veld Type 26, False Karroid Broken Veld (Acocks, 1953 and 1975) and are characterised by low growing dwarf scrub with shrubs mainly along the watercourses and at Tierberg also on the koppies. The nest sites (Figs 4 and 5) are in bare areas in relatively close proximity to water. The soil in which the nests had been excavated was semi-non-friable to non-friable with a high enough clay element to make it malleable when mixed with water.

Daily flight pattern and sheltering behaviour

On a hot sunny day the period of activity of *Paravespa (G.) mima* seems to be from mid-morning to late afternoon. At night, before and after the period of daily activity, and during periods of inactivity resulting from the sky being overcast females were observed to shelter in their nests head uppermost a short distance below the ground surface (Fig. 6).

Plant visiting

No flower visiting records were obtained. However, a nesting female which was being observed flew from her nest to some low bushes of *Pteronia* sp. (Compositae) which were in flower. She did not appear to be interested in the flowers but rather to be hunting. Her search was unfortunately unsuccessful and she flew further afield.

Male behaviour

One male only was observed in the nesting area at Tierberg. He was seen to be making a regular inspection of all the nests in the area. After the nests had been covered with glass jars in order to capture the females when they left their nests the male continued his visits undeterred. The presence of a female in such a jar caused the male to become extremely agitated.

Identification of the prey

Somewhat in excess of fifty prey caterpillars were recovered from six cells of *Paravespa (G.) mima* (see Table 3). Of these caterpillars slightly over thirty were in a good state of preservation, the remainder being partly eaten, shrivelled or otherwise damaged. At least four species were

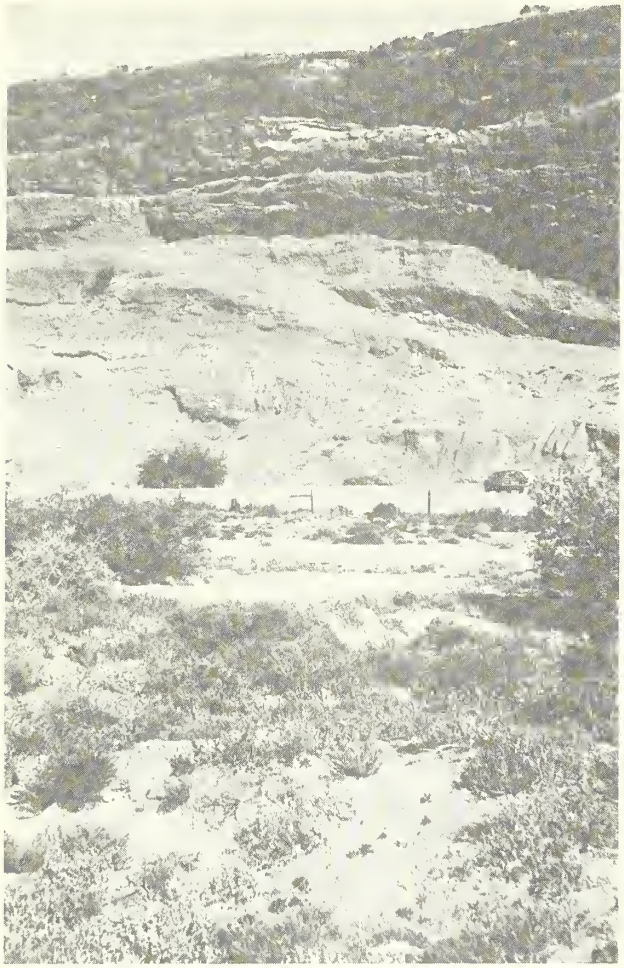

Fig. 4. Nesting area of *Paravespa (G.) mima* Giordani Soika at Onverwacht, 6.vii.1987. The nest site was in the bare area in the middle distance.

represented. The key to larvae of Lepidoptera adapted from Forbes (1923) by Brues, Melander and Carpenter (1954) was used in an attempt to identify the caterpillars to familial level. All the specimens were tentatively determined as belonging to the Noctuidae though a considerable element of doubt remains.

The most commonly represented species, Species A, was relatively short and broad, and pale-coloured with a virtual absence of any markings. Prolegs were absent from abdominal segments 3 and 4 but were well developed on 5, 6 and 10 and bore a longitudinal band of uni-ordinal crochets. This was the only species recovered from Nest 3 and Nest 8 but was also

Fig. 5. Nesting area of *Paravespa (G.) mima* Giordani Soika at Tierberg, 26.xi.1987–5.xii.1987. The nesting sites were in close proximity to the figure in the middle distance.

Fig. 6. Turret of Nest 14 of *Paravespa (G.) mima* Giordani Soika to show the sheltering position of the female (× 1).

represented by two specimens in Nest 12. Species B was of more usual proportions than Species A. It was pale-coloured with, however, an anterior and a posterior dark transverse stripe dorsally on the majority of the segments. It too had prolegs only on abdominal segments 5, 6 and

10 and uni-ordinal crochets arranged in a longitudinal band. It was the only species present in Nest 1 (at Onverwacht) but was also represented in Nest 2 and Nest 12 (both at Tierberg) by two and three specimens respectively. Species C bore fleshy papillae on the thorax and abdomen. It too was pale-coloured. Prolegs were present on abdominal segments 3–6 and 10 and bore uni-ordinal crochets arranged in a longitudinal band. The species was represented in Nest 2 and Nest 12 by one and two specimens respectively. Species D was non-papillate and pale-coloured. Prolegs and crochets were as in Species C. The species was represented in Nest 2 and Nest 12 by three and one specimens respectively.

TABLE 3

Provision of *Paravespa (G.) mima* Giordani Soika from five nests.

Nest No.	Locality	Cell	Number of prey	Size of prey mm	Identity of prey
1	Onverwacht	1	3	8,2–11,3 av. 9,5	Sp. B.
2	Tierberg	2	6	5,3–9,6 av. 6,9	Sp. B. (2) Sp. C. (1) Sp. D. (3)
3	Tierberg	1 2	*c* 12 14	not measured—condition poor 5,3–11,7 av. 7,9	Sp. A. Sp. A.
8	Tierberg	? of 4	?	not measured—condition poor	Sp. A.
12	Tierberg	1	8	7,1–11,5	Sp. A. (2) Sp. B. (3) Sp. C. (2) Sp. D. (1)

As is evident above, some cells were found to be provisioned with a single species of caterpillar, others with a mixture of up to four species. Caterpillar lengths ranged between 5,3–11,7 mm. Several sting lesions were present on each prey, distributed on the underside of thoracic segments 1–3 and abdominal segments 1–4. In Nest 3 (Cell 1) some of the caterpillars were in a semi-pupated state.

Prey provenance

No indication has, as yet, been found of what are the forage plants of the caterpillars preyed upon by *Paravespa (G.) mima*. The appearance of at least the most commonly utilized caterpillar, Species A, suggests that it occurs in protected situations.

Description of the nest

The nest of *Paravespa (G.) mima* consists of a multicellular subterranean burrow surmounted by a mud turret (Figs 7–12). The turret which is constructed from mud pellets is

Fig. 7. Tubular turret of Nest 12 of *Paravespa (G.) mima* Giordani Soika (× 1). Note discarded pellets to left of turret.

either in the form of a funnel or a curved tube. The subterranean burrow consists of a relatively long vertical main shaft terminating in a cell, and several secondary shafts each of which after leaving the main shaft at a gentle angle curves downwards steeply to end in a vertical cell. All the cells lie at the same depth. The cell diameter is equal to or only slightly in excess of that of the shaft. The sides of a cell are parallel and the end is truncate. There is no subdivision of the cell into compartments.

Method of construction of the nest, oviposition and provisioning

Water which is required for nest excavation is fetched in the crop. At Tierberg water was being collected from pools in the river bed.

The turret is constructed early in nest excavation (Figs 13 and 14). Pellets are laid down around the shaft initial in such a way that the base of the turret will have the same inner diameter as that of the shaft, that is 6,5–9,0 mm (average 7,7 mm, sample of 19). Initially pellets are laid down regularly so that the base of the turret is in the form of a vertical cylinder, smoothed on the inside and rough on the outside. As turret construction proceeds, however, the manner in which the pellets are laid down changes in one of two ways. Either the diameter is rapidly increased to form a stalked funnel with an almost horizontal rim (Figs 8 and 10) with a distal diameter of 17–31 mm (average 22,9 mm, sample of 9) or the original diameter is maintained and the turret curves over to one side and is continued sub-horizontally so that the lower lip which is somewhat longer than the upper lip extends 30–43 mm (average 34,5 mm, sample of 4) from the shaft opening (Figs 7 and 9). The pellets used in the construction of funnel-shaped turrets are closely packed and no interstices are left open whereas those used in the construction

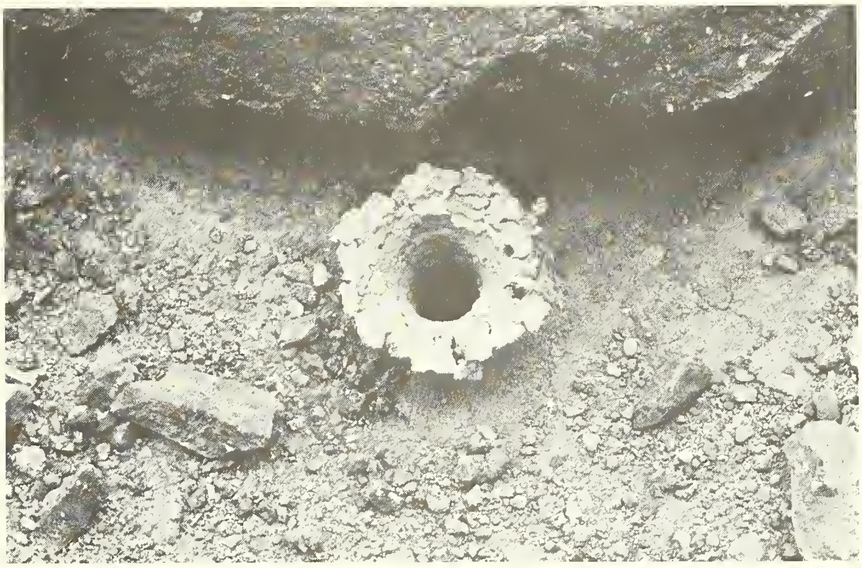

Fig. 8. Funnel-shaped turret of Nest 14 of *Paravespa (G.) mima* Giordani Soika from above (× 1).

Fig. 9. Tubular turret of Nest 12 of *Paravespa (G.) mima* Giordani Soika from the side (× 1).

Fig. 10. Funnel-shaped turret of Nest 1 of *Paravespa (G.) mima* Giordani Soika from the side (× 1,8).

of curved turrets are only closely packed on the underside of the tube, a large number of interstices being left open on the upper side.

After the completion of the turret shaft sinking continues vertically and further pellets extracted from the excavation are discarded either in a distinct pellet dropping area in close proximity to the nest (Fig. 7) or randomly at some distance from the nest. This difference in technique seems to be an individual variation. One female observed at Tierberg was away from the nest for 31–36 seconds when fetching water and between fetching each load of water extracted 2–3 pellets and in addition used some water and spent some time in stabilizing the shaft

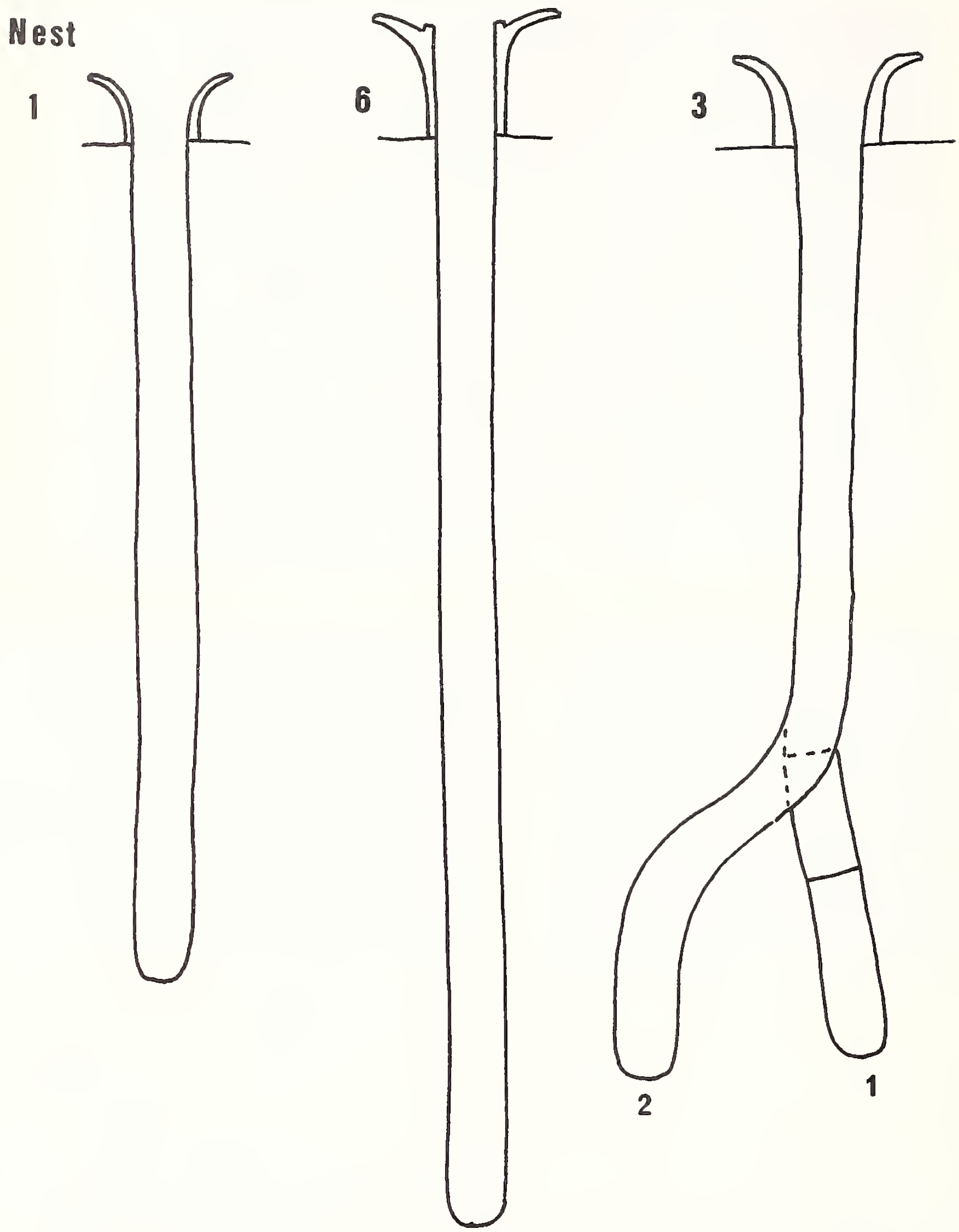

Fig. 11. Vertical plans of turrets and underground workings of *Paravespa (G.) mima* Giordani Soika (× 1).

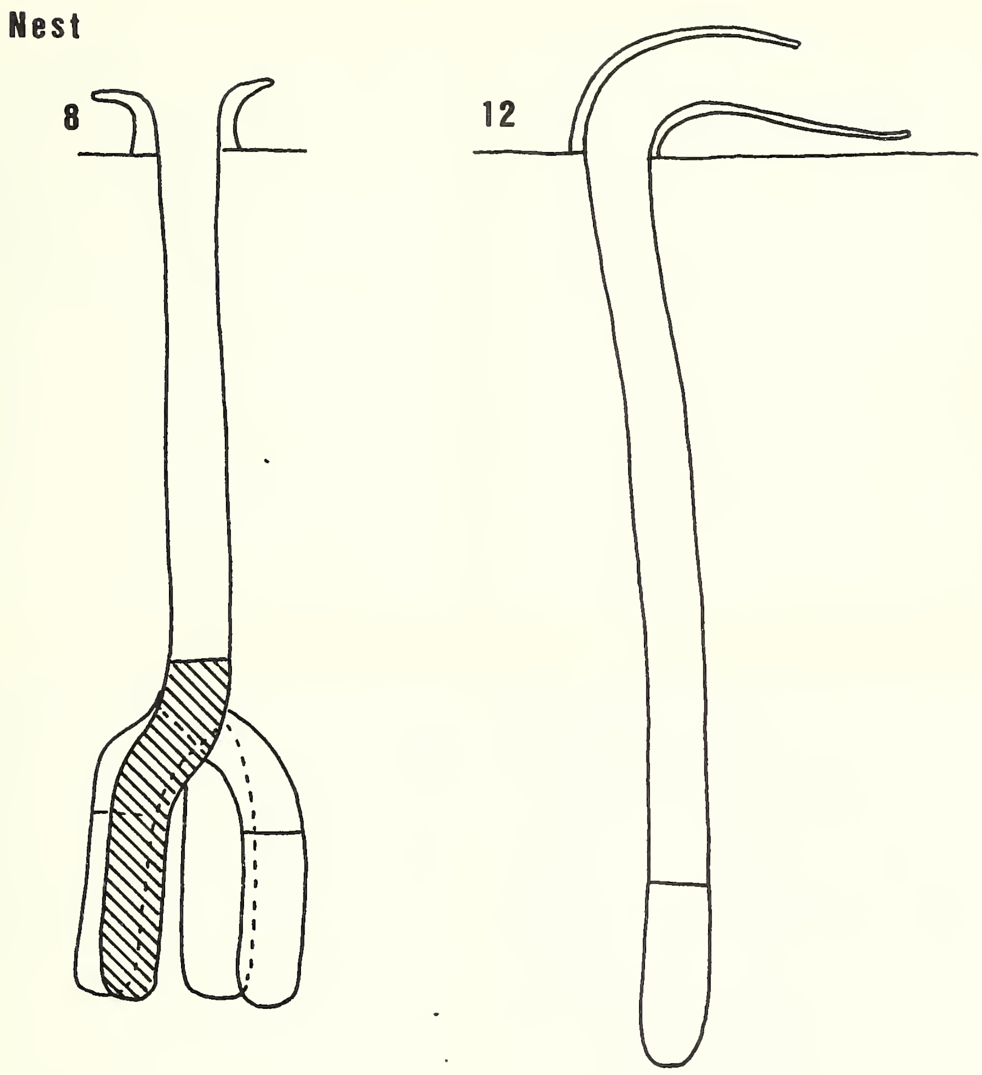

Fig. 12. Vertical plans of turrets and underground workings of *Paravespa (G.) mima* Giordani Soika (× 1); Crosshatching represents leaf cells of *Megachile stellarum* Cockerell.

walls. The shaft walls are smoothed with water so that their surfaces which would otherwise be coarse and gritty due to the nature of the substrate become as though plastered. Whilst the shaft is relatively shallow the wasp, head down in the shaft, can be observed moving up and down and rotating whilst performing this smoothing.

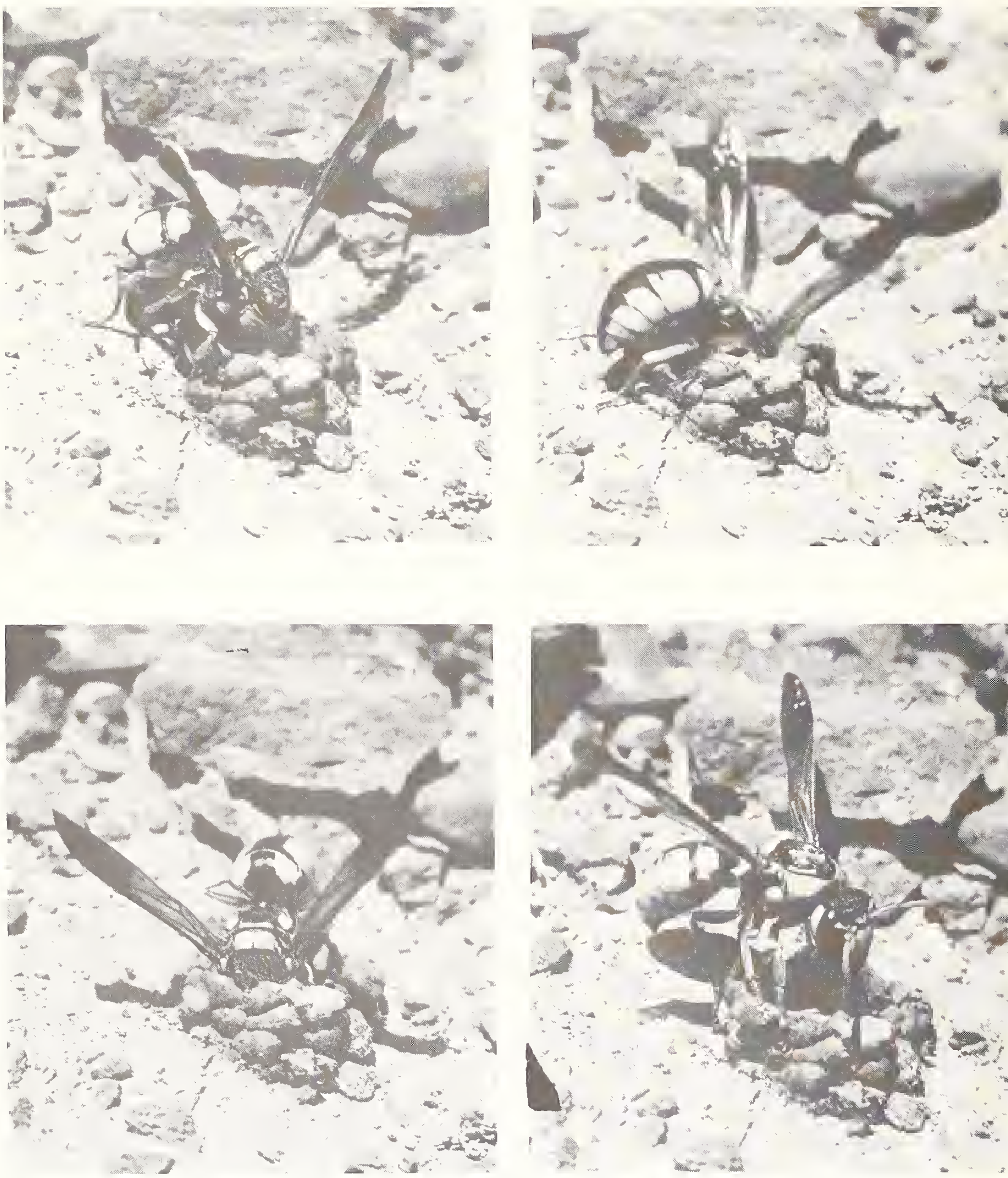

Fig. 13. A female *Paravespa (G.) mima* Giordani Soika constructing the turret of Nest 14 (× 1,6).

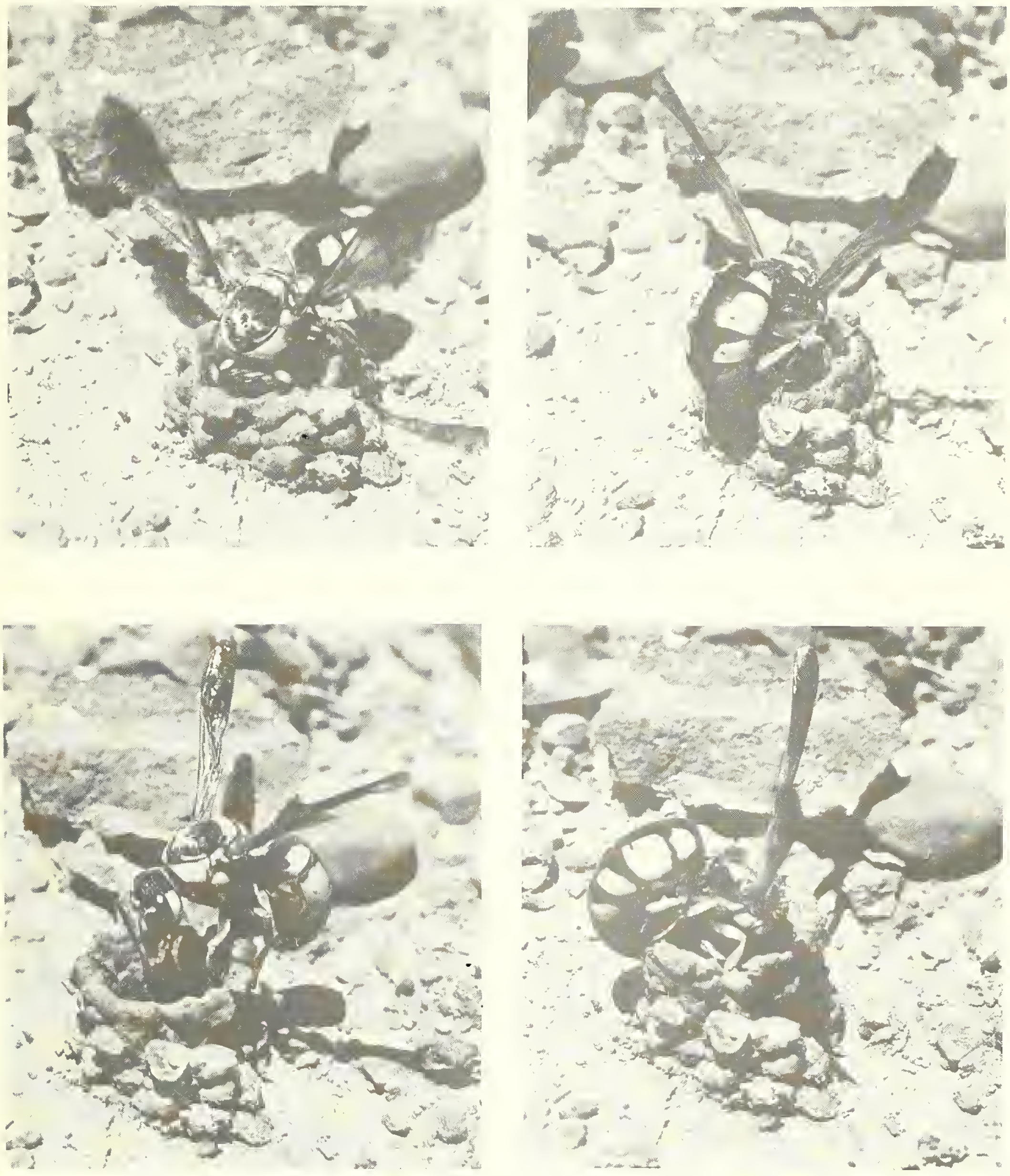

Fig. 14. A female *Paravespa (G.) mima* Giordani Soika constructing the turret of Nest 14 (× 1.6).

The first cell when ready for use is not distinct from the main shaft as a cell is only marginally greater in diameter than the shaft leading to it and as it has parallel sides and the distal end is sub-truncate. The average diameter of a provisioned cell is greater than that of the shaft leading to it by only 1,1 mm (range 0–1 mm, sample of 11).

After oviposition and provisioning has taken place the cell is sealed with a barely discernable mud plate and the portion of the shaft close to the cell is filled with earth for a short distance and then a mud seal is constructed between it and the rest of the shaft. Immediately above this seal a secondary shaft is excavated (Fig. 11: Nest 3). This shaft curves to one side for a short distance before turning sub-vertically downwards, the sub-vertical portion constituting a cell.

Nineteen nests were investigated. Of these nests three were one-celled, two two-celled and one four-celled. Of the remaining 13 nests nine had been usurped by megachilid bees before the completion of a cell, a tenth had been usurped by an *Ammophila* species, probably *A. braunsi* (Turner) and the remaining three neither had provisioned *Paravespa (G.) mima* cells nor had they been usurped (Table 4).

Nests in which a cell or cells had been constructed varied in depth from 102–125 mm.

Final sealing of nests was not observed.

TABLE 4.

Details pertaining to 19 nests of *Paravespa (G.) mima* Giordani Soika. Nest 1 investigated at Onverwacht, Oudtshoorn, 9.xii.1986 and nests 2–19 investigated at Tierberg, Prince Albert district, 27.xi.1987–5.xii.1987.

Nest No.	Nature of turret	No. of cells	Cell no.	Nature of cell contents
1	funnel	1	1	3 caterpillars
2	funnel	2	1	fully grown *Paravespa (G.) mima* larva in cocoon
			2	6 caterpillars and *Paravespa (G.) mima* larva
3	funnel	2	1	*c* 12 caterpillars and *Paravespa (G.) mima* larva
			2	14 caterpillars and *Paravespa (G.) mima* larva
4	funnel	—	—	caterpillar and egg of *Ammophila* sp.
5	funnel	—	—	—
6	funnel	—	—	—
7	funnel	—	—	petal cell of *Megachile aliceae*
8	funnel	4	?	fully grown *Paravespa (G.) mima* larva in cocoon
			?	fully grown *Paravespa (G.) mima* larva in cocoon

Nest No.	Nature of turret	No. of cells	Cell no.	Nature of cell contents
			?	several caterpillars, condition poor
			4	3 leaf cells of *Megachile stellarum*
9	curved	—	—	—
10	curved	1	1	leaf cells of *Megachile stellarum*
11	curved	—	—	petal cell of *Megachile aliceae*
12	curved	1	1	8 caterpillars and *Paravespa (G.) mima* larva
13	curved	—	—	—
14	funnel	—	—	leaf cell of *Megachile stellarum*
15	curved	—	—	2 leaf cells of *Megachile stellarum*
16	funnel	—	—	leaf cell of *Megachile stellarum*
17	—	—	—	4 leaf cells of *Megachile stellarum*
18	funnel	—	—	2 leaf cells of *Megachile stellarum*
19	curved	—	—	3 leaf cells of *Megachile stellarum*

Reaction to rain damage

A heavy downpour in which nest turrets were damaged occurred one afternoon during the period when *Paravespa (G.) mima* was being observed at Tierberg. The next day a wasp was observed repairing the turret of Nest 14, the rim of which had been damaged by the rain. Turrets of other nests had been completely washed away but as these nests had been usurped by megachilid bees before the storm it is not known what the response of *P. (G.) mima* would be to such extensive damage. It is, however, of interest that several "double turrets" were found. It is possible that the building of a second rim within the first may in some instances be a response to damage to the original turret.

Cocoon

The fully grown larva of *Paravespa (G.) mima* spins a cocoon which is closely bonded to the cell walls and entirely fills the cell. The cocoon is capped with the head capsules of the prey caterpillars which separate it from the mud plate closing the cell.

Associated insects

Megachilid bees had usurped a high percentage of the nests of *Paravespa (G.) mima* investigated at Tierberg between 26.xi.1987 and 5.xii.1987. Of the eighteen nests investigated nine, that is 50 %, had been usurped. All but one of these nests, the four-celled Nest 8, had been invaded before nest provisioning by *P. (G.) mima* . These nests had not been abandoned by the

wasps before take over by the bees. Wasps which were actively working on their nests were seen to be severely harassed by the bees resulting in their becoming confused and eventually abandoning their nests. The activities of the megachilid bees had therefore resulted in a total loss of nesting effort on the part of the original nest owners.

Two species of megachilid bees were involved, *Megachile stellarum* Cockerell in seven instances and *Megachile aliceae* Cockerell in two instances. *M. stellarum* has previously been recorded nesting in burrows of *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974: 204–206, Fig. 8), *Parachilus insignis* (Gess and Gess, 1976: 98) and *Ceramius lichtensteinii* (Klug) (Gess and Gess, 1980: 78) at Hilton near Grahamstown, Eastern Cape Province. In all instances the bee's cells, constructed from pieces cut from leaves, were arranged serially. In the nests of *Paravespa (G.) mima* , one to five leaf cells were constructed, in all instances positioned at the inner end of the excavation. Towards the outer end of the excavation a seal (Fig.16: Nest 16) was constructed, like the cells, from leaf pieces. Pollen from the provision was examined and on comparison it was found to be a mixture derived from *Pentzia incana* and "mesems".

Megachile aliceae has previously been recorded nesting in burrows of *Parachilus insignis* (Gess and Gess, 1976: 98) at Hilton near Grahamstown, Eastern Cape Province and in burrows of *Ceramius nigripennis* Saussure (Gess and Gess, 1986: 173–174) at Mesklip, near Springbok, Namaqualand. The cells of this bee are constructed from pieces of petal. At Mesklip and Tierberg the petals used were orange. The cells of this species seem to follow the shape of the cavity, those constructed in cells of *Ceramius nigripennis* being "pot" shaped and those constructed in burrows of *P. (G.) mima* being cylindrical. In the nests of *P. (G.) mima* a lower provisioned cell and an upper "cell" filled with earth had been constructed and in addition in one nest an earth fill had been added in the shaft above.

One of the nests of *P. (G.) mima* (Fig. 15 and Fig. 16: Nest 4) was found to have been filled to the mouth with fine gravel. On investigationn the underground workings were found to consist of a main shaft of depth 132 mm. The bottom of this shaft had been filled with gravel (particle size up to 5 mm) to a depth of 56 mm, above which had been placed a noctuid caterpillar to which an egg had been attached. The caterpillar occupied a cell 20 mm long sealed above with very fine gravel which filled the remainder of the shaft and the turret. It seems probable that this was a nest of *Ammophila braunsi* (Turner) as this is the only wasp nesting in pre-existing cavities in the ground known to the authors to provision with noctuid caterpillars. The nesting of *A. braunsi* was investigated by the authors at Hilton in the summer of 1983/1984. There it was found to nest in pre-existing cavities, the burrows of *Parachilus insignis*, and to provision its cells with noctuid caterpillars. *A. braunsi* was collected in the nesting area of *P. (G.) mima* at Tierberg where it was not uncommon.

DISCUSSION

The division of the cell into an egg compartment and a pantry compartment was first described for *Parachilus insignis* (Gess and Gess, 1976). It was noted by Gess and Gess that this behavioural character marked off the nesting of this species from that known at that time for other Eumenidae . The present investigations of the nests of *Parachilus capensis* and *Parachilus major* show that the division of the cell into an egg compartment and a pantry compartment or compartments is not a behavioural character exclusive to the species *P. insignis* but is of wider occurrence within the genus *Parachilus*. Whether or not it is characteristic of the genus as a

Fig. 15. Turret of Nest 4 of *Paravespa (G.) mima* Giordani Soika filled with gravel by the nest usurper, *Ammophila* sp. (× 1).

whole awaits the discovery of the nesting of the other species of the genus, however, it seems likely that it will be found to be so. The present investigation of the nesting of *Paravespa (Gestrodynerus) mima* adds a species of an additional genus to the list of those known not to divide their cells.

The investigations of the nesting of *P. capensis* , *P. insignis* and *P. major* show that these species are separable from each other on characters of nest architecture (Figs 1, 17 and 3). The turrets of the three species are distinct. That of *P. insignis* is little more than a collar, that of *P. capensis* is a vertical funnel with the diameter of the distal opening considerably greater than that of the base (1:2,5 and 1:3 in the two nests discovered) and that of *P. major* is a sub-vertical to sloping tube with the diameter of the distal opening not markedly greater than that of the base (not more than 1:1,5 in the sample of seven) so that it cannot be considered to be a funnel.

P. insignis excavates burrows having apparently no more than one or two cells (sample of 35) whereas burrows of *P. major* with up to four cells have been found (sample of 7). As only two nests of *P. capensis* have been located a statement on cell numbers is premature. The single completed cell of *P. capensis* differed markedly from those of the other two species, which have a single pantry compartment per cell, in having three pantry compartments.

The main shaft in all three species terminates in the first cell, however, *P. major* (Fig. 3) differs from *P. capensis* (Fig. 1) and *P. insignis* (Fig. 17) in the gradient of both the shaft and the cell. The main shaft of the first descends gently and then curves downwards steeply so that the gradient of the cell is steeper than that of the shaft whereas in the other two species the main shaft descends vertically and then terminates in a sloping cell. Additional cells in burrows of *P. major* terminate secondary shafts in gradient similar to that of the first cell and each leaves the

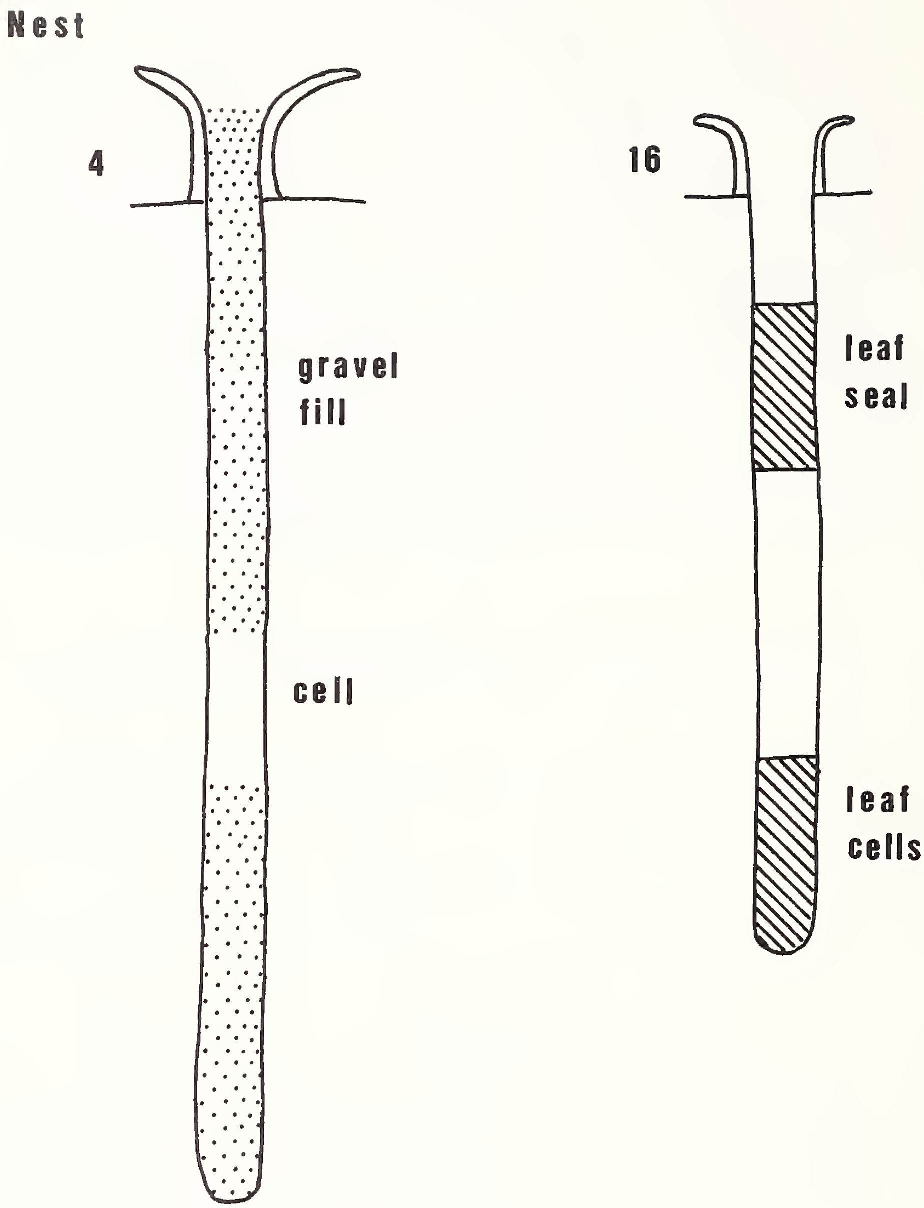

Fig. 16. Vertical plans of turrets and underground workings of *Paravespa (G.) mima* Giordani Soika (×1); Nest 4 usurped by *Ammophila* sp. and Nest 16 by *Megachile stellarum* Cockerell.

main shaft nearer to the shaft opening than that preceeding it in such a way that the cells come to lie with their long axes more or less parallel to each other. The secondary shaft/second cell in burrows of *P. capensis* and of *P. insignis* by contrast leaves the main shaft in such a way that it diverges from the first cell, that is the upper ends of the cells are close together and the lower ends widely spread to form an inverted "V".

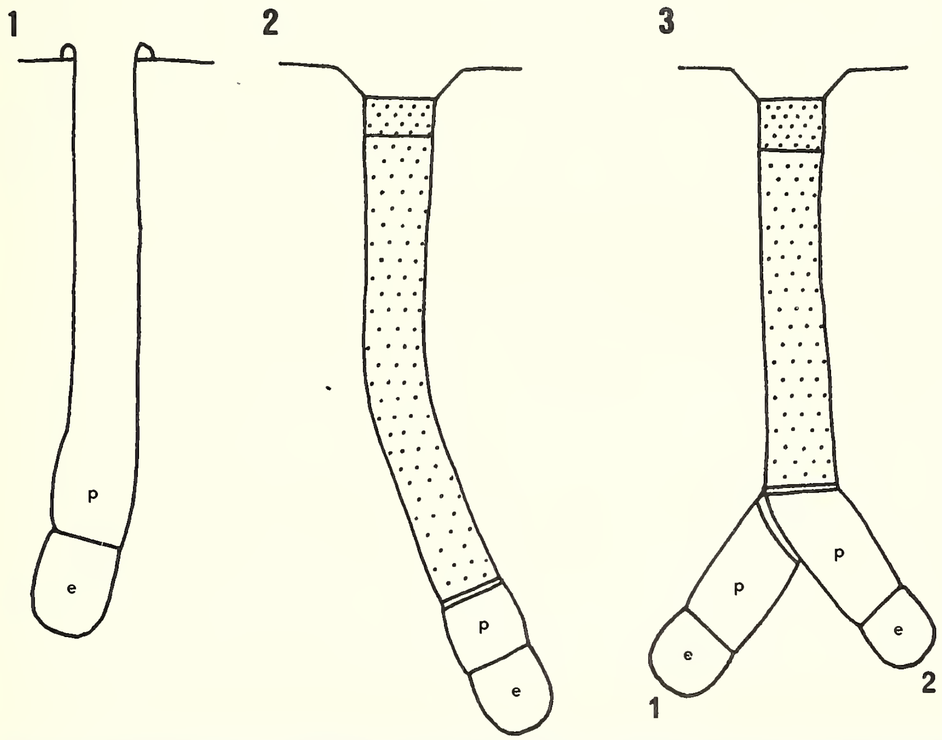

Fig. 17. Vertical plans of three nests of *Parachilus insignis* (Saussure) (× 1) to show : 1. nest turret 2. a single celled sealed nest and 3. a two celled sealed nest. Hilton. 29.x.1973–27.xii.1973. e–egg compartment; p–pantry compartment.

Psychidae appear very rarely to be taken as prey by aculeate wasps. No instances are given by Iwata (1976) and only a single record is listed by Krombein *et alia* (1979) for the relatively well studied North American fauna. This concerns a species of Eumenidae, *Stenodynerus fundatiformis fundatiformis* (Robertson) the nesting of which was studied in Florida by Krombein (1964). Prey recovered from the nests consisted of both lepidopterous and coleopterous larvae, the Lepidoptera being represented by one species of each of four families including Psychidae. It was suggested that the wasps were exploring a particular microhabitat and that the species preys upon larvae which seek protection by enclosing themselves in various ways, for example in cases or rolled leaves. The taking of psychid caterpillars by the three species

of *Parachilus* would, from the above, appear to represent a highly unusual prey preference, all the more so as prey selection seems to be absolutely restricted to these caterpillars. Remarkable too is the fact that all three wasps appear to prey upon the same two caterpillar species.

Though the nesting biology of only three of the ten species of *Parachilus* Giordani Soika has been studied, the consistency shown by *P. capensis*, *P. insignis* and *P. major* with regard to the subdivision of the cells into egg and pantry compartments and the taking of larval Psychidae for provisioning the cells suggests that the genus is a natural one and clearly distinguishes it from other ground-nesting odyneroid genera including *Paravespa* Radoszkowski, exemplified in the present study by *P. (Gestrodynerus) mima*.

The construction by *P. (G.) mima* of turrets of two distinct architectural styles is remarkable and that the two forms should have been constructed by wasps belonging to the same population is even more remarkable. It is of note that the single male which was patrolling the nesting area visited nests of both forms indiscriminately confirming that the builders of these nests were truly of one species.

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New species of the genus *Celonites* Latreille (Hymenoptera: Masaridae) from South Africa.

by

F. W. GESS

(Albany Museum, Grahamstown)

ABSTRACT

Descriptions are given of four new species of southern African *Celonites* Latreille, namely *bergenwahliae* and *wahlenbergiae* from the Clanwilliam District of the western Cape Province and *davidi* and *peliostomi* from Namaqualand.

INTRODUCTION

The writing of the present paper is occasioned by the need to provide names for three hitherto undescribed species of *Celonites* included in a paper on flower visiting by masarid wasps in southern Africa to be published shortly by S. K. Gess and F. W. Gess. The opportunity is taken to describe also a species for which no ethological data are as yet available. All four species belong to the assemblage termed by Richards (1962) the "Group of *C. wheeleri* Brauns" which includes all the known South African species of the genus and is characterized by the marked separation of the lateral lamellae of the propodeum from the median part of that body segment.

With the exception of one male paratype and one female paratype of each of the following three species, *C. bergenwahliae*, *C. peliostomi* and *C. wahlenbergiae*, deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, all the type material is in the Albany Museum, Grahamstown.

TAXONOMIC DESCRIPTIONS

Celonites peliostomi sp. nov.

Female (Figs 1 and 3)

Black; a spot on each side of face above ocular sinus and end of V-shaped raised frontal keel, very occasionally a small spot or streak on upper edge of each arm of frontal keel, posterior margin of pronotum, humeral angles, an elongate spot on each prepectus, base and apex of each tegula, almost entire upper and lower faces of propodeal lamellae, elongate wedge-shaped postero-lateral markings on tergites 1–5, sometimes a weakly defined median posterior triangular marking on tergite 5, small spots at distal ends of fore-femora and on proximal ends

of tibiae of all legs, *yellowish-white*; mandibles (other than at base), underside of antennal clubs, greater part of tegulae, hind margin of scutellum medially, metanotum medially, transverse bands between black basal bands and pale-coloured postero-lateral markings on tergites 1–5, sternites, most of tibiae and tarsi, *reddish-brown*.

Wings lightly browned.

Length 6,5–7,5 mm; length of fore wing 4,7–5,0 mm; hamuli 7.

Head (Fig. 1), pronotum, mesopleura, mesonotum, scutellum and dorso-lateral areas of propodeum coarsely and densely punctured; punctures on sides of pronotum, mesonotum, sides of scutellum and upper regions of mesopleura tending to form longitudinal striae.

Clypeus with a V-shaped raised keel which starts near but below antennal sockets and has its point on the midline a little below centre of disc; frons above antennae with a transverse V-shaped raised keel which starts in upper third of ocular sinuses and has its point on the midline at level of upper margin of antennal sockets.

Scutellum medially convex, strongly raised above level of mesonotum and with a wide crenulate anterior furrow.

Propodeal lamella (Fig. 3) of each side inclined at about 45 degrees to horizontal, narrow, bluntly pointed distally, with outer edge largely smooth and disc translucently punctured, separated from the median part of the propodeum by a proximally straight slit; median part of propodeum with ventro-lateral area bordering slit on each side markedly angled at edge and smoothly surfaced and shining, with angular tubercle situated dorsally on each side moderately strong and with general posterior surface (including concave declivity) longitudinally (vertically) striate.

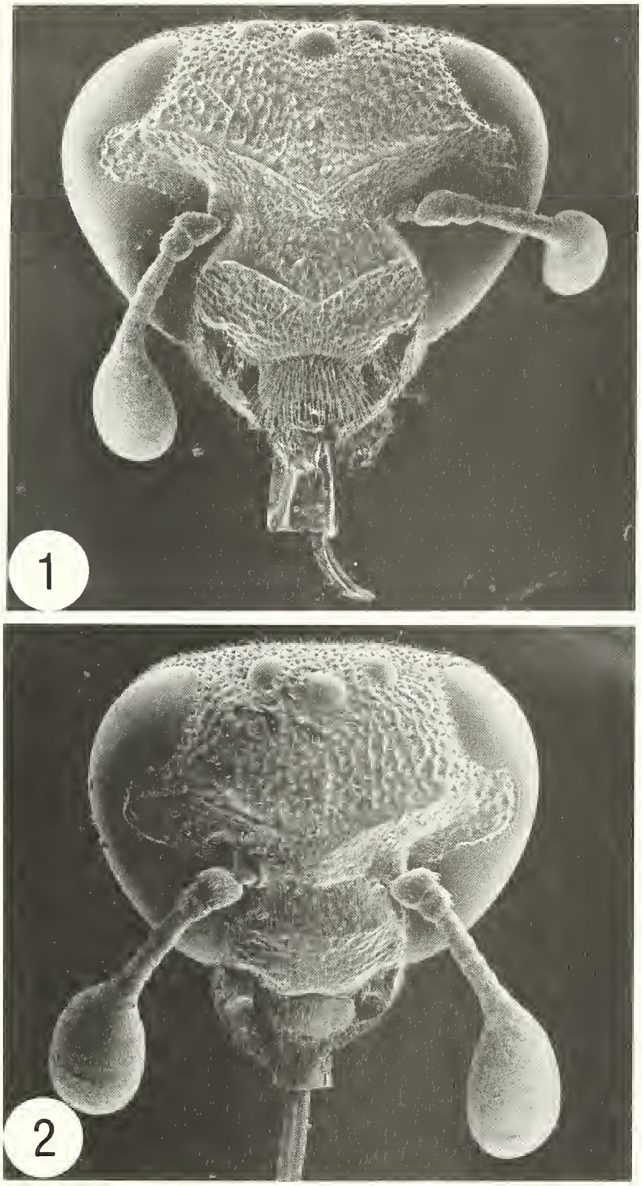
Gastral tergites closely, finely and somewhat superficially punctured, weakly shining, with their posterior margins mostly smooth; tergites 1–5 with at least some of the posterior outer angles (most commonly those of tergites 4 and 5) moderately projecting; tergite 6 with median part roundly produced, emarginate before sides. Gastral sternites shining; sides and postero-lateral corners of sternite 2, a broad transverse proximal band on and postero-lateral corners of sternites 3–5, and all of sternite 6 (excepting a smooth region along midline) with fine shallow punctures.

Male (Figs 2, 4 and 5)

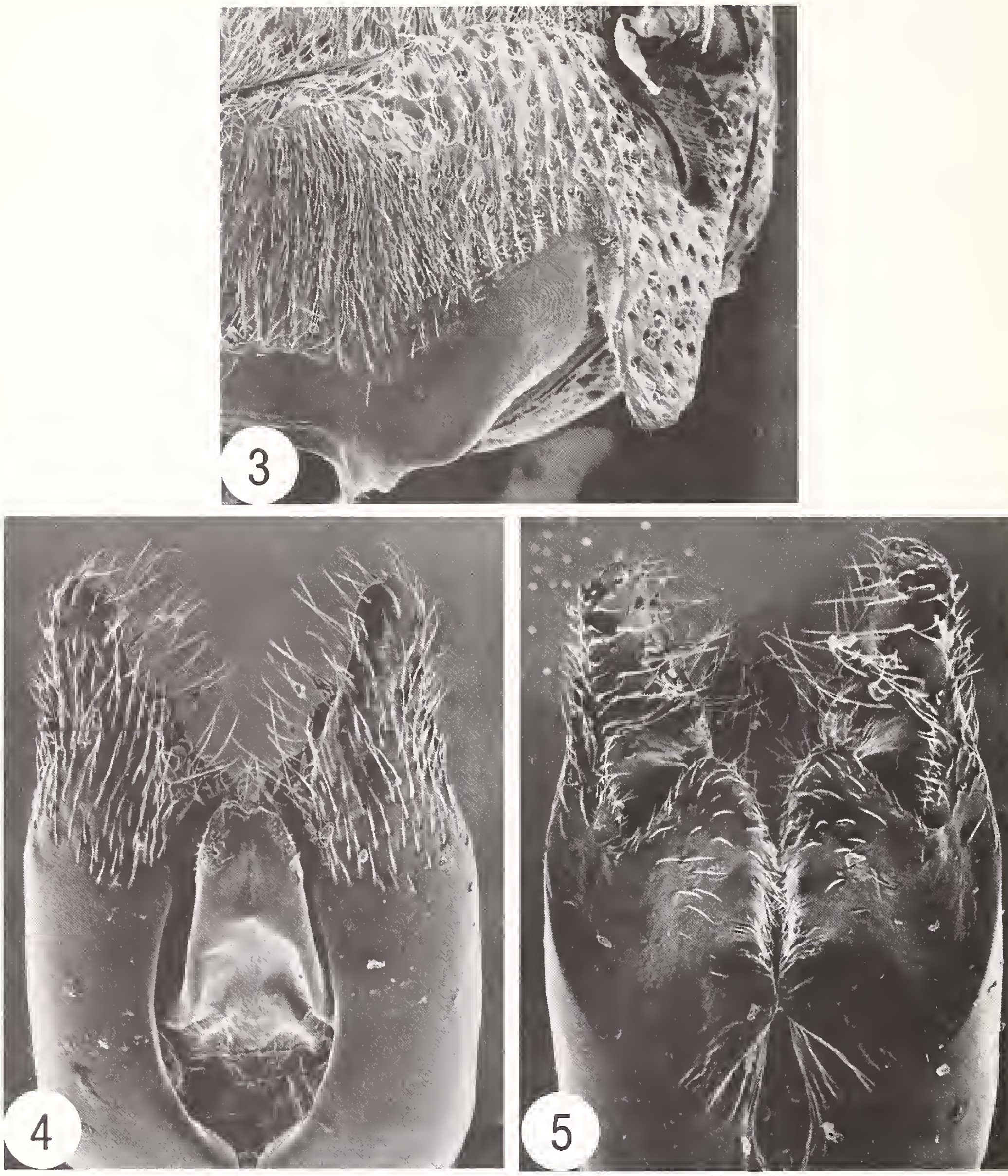
Colouration very similar to that of female differing only with regard to the *yellowish-white* markings on the head. These markings are: a large irregularly-shaped spot (absent in female) on disc of clypeus basally, a spot on each side of face within (not above as in female) ocular sinus; usually (not only occasionally as in female) a small spot or streak on upper edge of each arm of V-shaped frontal keel.

Length 7,2–7,6 mm; length of fore wing 4,4–4,7 mm; hamuli 6–7.

Structure much like that of female differing most noticeably with respect to the following: antennal club both longer and wider with individual segments less discernible and with three sensory depressions beneath; eyes closer below; clypeus narrower and with V-shaped raised keel almost obliterated, only its ends indistinctly indicated; frons with V-shaped raised keel weak medially; tergites with posterior outer angles more strongly projecting; tergite 7 compared to tergite 6 of female with median part much less rounded, subtruncate, and with lateral emarginations deeper (due to stronger development of posterior outer angles).



Figs 1 and 2. *Celonites peliostomi* sp. nov.: frontal view of head of female (Fig. 1) and of male (Fig. 2) (both × 25).



Figs 3, 4 and 5. *Celonites peliostomi* sp. nov.: dorsal view of right half of propodeum of female showing lamella (Fig. 3) (× 65); subdorsal view (Fig. 4) and subventral view (Fig. 5) of genitalia of male (both × 100).

Genitalia (Figs 4 and 5); parameres gently tapering towards their ends which are rounded and entire; they and volsellae with scattered fine hairs.

Material examined: Cape Province: Namaqualand, Springbok, Hester Malan Nature Reserve, 15–21.x.1987 (F. W. and S. K. Gess), Holotype female, Allotype male, 37 female Paratypes and 2 male Paratypes (all in flowers of *Peliostomum virgatum* E. Mey ex Benth., Scrophulariaceae); same locality, dates and collectors, 5 female Paratypes (all in flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae); same locality, dates and collectors, 1 male Paratype (in flower of *Aptosimum lineare* Marl. and Engl., Scrophulariaceae); same locality, dates and collectors, 1 female Paratype (Malaise trap), same locality, 10–12.x.1988 (F. W. and S. K. Gess), 3 male Paratypes, same locality and dates (D. W. Gess), 1 male Paratype; [Cape Province:] Namaqualand, [Springbok] 2917 DB, Hester Malan N[ature] R[eserve], 30.x.1987 (M. Struck), 1 female Paratype (on *Peliostomum virgatum*).

Etymology: The name, in the genitive singular, is formed from the generic name of the plant, *Peliostomum virgatum* E.Mey ex Benth. (Scrophulariaceae), in the flowers of which the wasp was most commonly found foraging for nectar or nectar and pollen, and serves to draw attention to the floral association.

C. peliostomi sp. nov. may be grouped with *C. capensis* Brauns and *C. humeralis* Richards in that the separation of the propodeal lamellae from the median part is by a deep, narrow, straight slit, not by a spiral slit ending in a circular emargination into which an extension of the median part of the segment projects strongly. However, in its possession of raised frontal and clypeal keels it is similar to *C. clypeatus* Brauns and *C. andrei* Brauns.

Celonites wahlenbergiae sp. nov.

Female (Figs 6 and 10)

Black; a narrow band along posterior margin of pronotum, variably developed postero-medial spots on tergites 2–4 (and occasionally also in a reduced size on 5), *yellowish-white*; distal half of mandibles, most of pronotum, whole of tegulae, at least extreme hind margins of scutellum and metanotum laterally (occasionally greater part of scutellum and also middle of metanotum), occasionally outer portions of propodeal lamellae, most of tergites 1–3 and occasionally part of tergite 4, whole of sternite 1 and sides of sternites 2 and 3, extreme distal ends of femora and whole of tibiae and tarsi of all legs, *reddish-brown*.

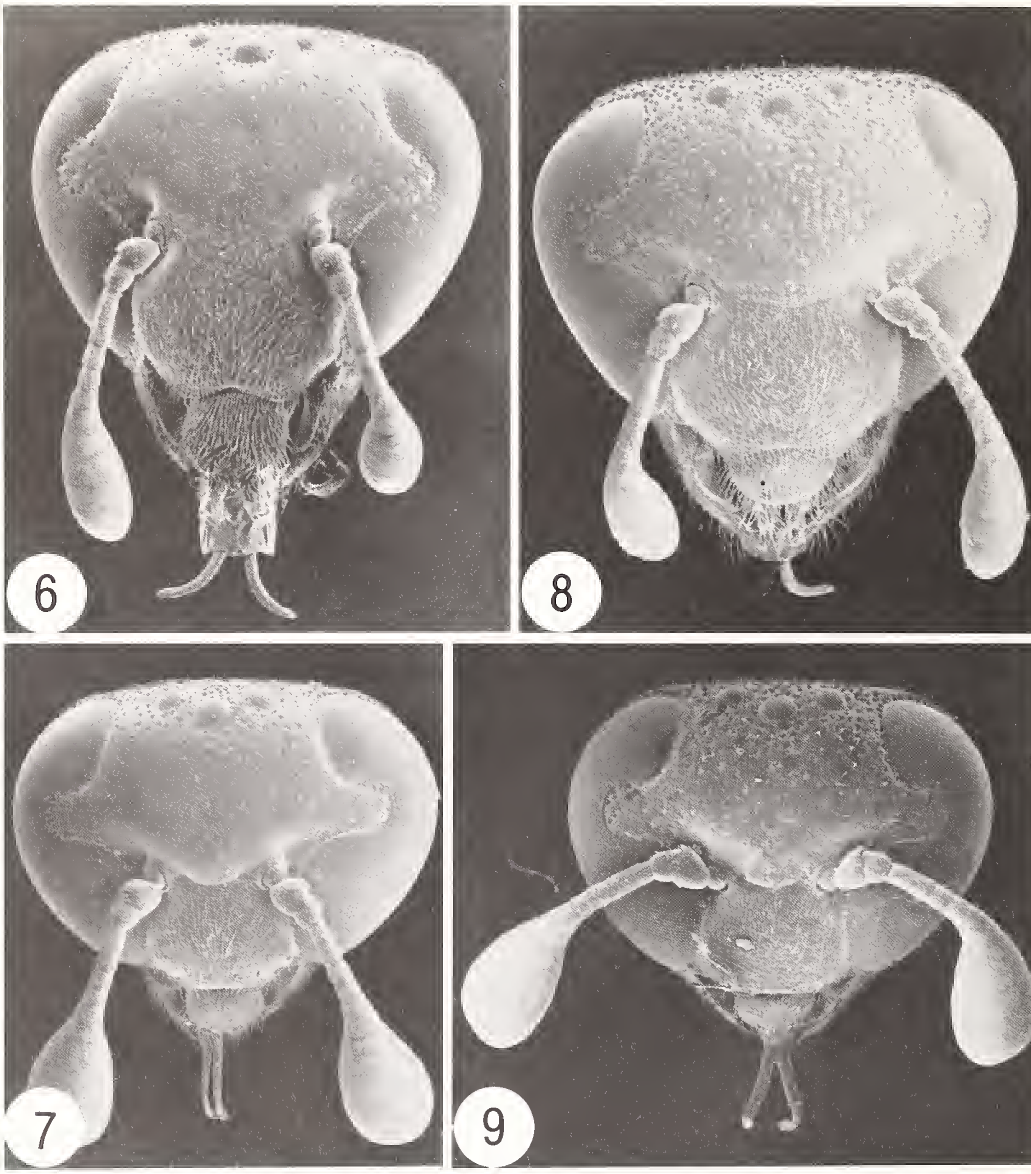
Wings lightly browned.

Length 7,3–8,3 mm; length of fore wing 4,7–5,3 mm; hamuli 7–8.

Head (Fig. 6) with puncturation of frons fine and very sparse on a microscopically longitudinally aciculate surface and constrasting with fine but denser puncturation on more strongly longitudinally aciculate to finely rugose surface of clypeus and moderate and dense puncturation of vertex. Pronotum, mesopleura, mesonotum, scutellum and dorso-lateral areas of propodeum coarsely and densely punctured; punctures on upper regions of mesopleura with a tendency to form not very noticeable striae.

Clypeus unmodified, its disc evenly convex and without any indication of a keel; frons with a feeble transverse prominence above antennae.

Scutellum medially convex, strongly raised above level of mesonotum and with a wide crenulate anterior furrow.



Figs 6 and 7. *Celonites wahlenbergiae* sp. nov.: frontal view of head of female (Fig. 6) and of male (Fig. 7) (both × 25).

Figs 8 and 9. *Celonites bergenwahliae* sp. nov.: frontal view of head of female (Fig. 8) and of male (Fig. 9) (both × 25).

Propodeal lamella (Fig. 10) of each side wide, broadly truncate distally, with outer edge gently convex, separated from the median part of the propodeum by an inwardly curving slit ending in a relatively large circular emargination; lateral projection of the ventral margin on each side of the median part of the propodeum with its hind edge transverse and its point narrowly rounded, as wide as long, and projecting across opening of curved slit at level of end of lamella.

Gastral tergites coarsely and densely punctured, with their posterior margins mostly smooth; tergites 1–5 with posterior outer angles moderately projecting; tergite 6 with median part roundly produced, very weakly emarginate before sides and with margin nowhere angular.

Gastral sternites shiny; sternite 2 with fine punctures scattered rather sparsely over surface; sternites 3–5 with close, moderate punctures in a broad transverse proximal band and on postero-lateral corners and with sternite 6 with similar punctures covering entire surface other than for smooth region along midline.

Male (Figs 7 and 11)

Colouration similar to that of female, differing most noticeably in the basically black (not reddish-brown) pronotum, in the reduction in the amount of reddish-brown on the tergites, and in the greater extent of yellowish-white markings.

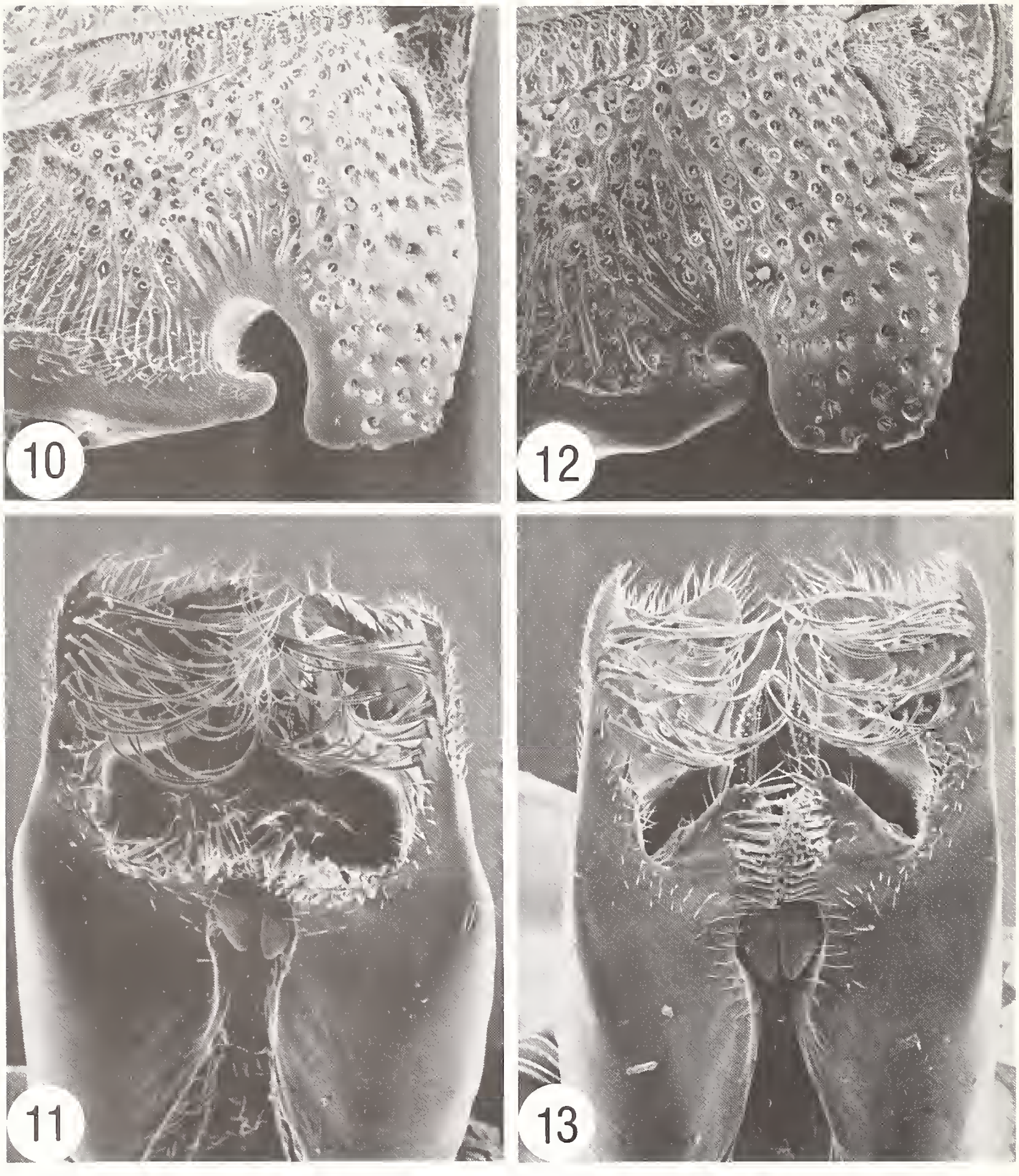
Black; whole of clypeus and labrum, occasionally a small median spot on face directly above clypeus, occasionally a spot within each ocular sinus or whole ocular sinus, an antero-medially expanded narrow band along posterior margin of pronotum and a spot on humeral angles (these markings occasionally meeting and fusing), occasionally a dot medially at apex of scutellum, postero-medial spots on tergites 1–5, *yellowish-white*; distal half of mandibles, whole of tegulae, usually extreme hind margins of scutellum and metanotum laterally, tergite 1 (other than anterior declivity), most of tergite 2, usually a postero-medial band on tergite 3 (i.e. usually not postero-lateral areas), whole of sternite 1 and antero-lateral areas of sternite 2, extreme distal ends of femora and whole of tibiae and tarsi of all legs, *reddish-brown*.

Length 6,5–7,3 mm; length of fore wing 4,2–4,8 mm; hamuli 7–8.

Structure much like that of female differing most noticeably with respect to the following: antennal club wider with individual segments less discernible and with three sensory depressions beneath; eyes closer below; clypeus narrower; frons with transverse prominence above antennae less feeble especially medially; tergites with posterior outer angles more strongly projecting; tergite 7 compared to tergite 6 of female with median part more widely rounded and with lateral emarginations much better developed (due to strong development of posterior outer angles).

Genitalia (Fig. 11); parameres wide and emarginate at their ends, furnished with long and strong inwardly directed curved hairs; each volsella with a subapical transverse band of short strong hairs; transverse hair bands on the right and left volsellae together forming a straight transverse band.

Material examined: Cape Province: Clanwilliam District, Clanwilliam Dam, 14.x.1987 (F. W. and S. K. Gess), 1 female Paratype (on ground) and 2 male Paratypes (in flowers of *Wahlenbergia* sp. A, Campanulaceae); same locality, 3–7.x.1988 (F. W. and S. K. Gess), Holotype female, Allotype male, 3 female Paratypes (1 in flower of *Wahlenbergia* sp. A, Campanulaceae) and 2 male Paratypes; same locality and dates (D. W. Gess), 4 female Paratypes and 6 male Paratypes; Clanwilliam District, 5 km W of Clanwilliam, road to Graafwater, 12.x.1987 (F. W. and S. K. Gess), 2 male Paratypes (on ground); same locality,



Figs 10 and 11. *Celonites wahlenbergiae* sp. nov.: dorsal view of right half of propodeum of female showing lamella (Fig. 10) (× 65); subventral view of genitalia of male (Fig. 11) (× 100).

Figs 12 and 13. *Celonites bergenwahliae* sp. nov.: dorsal view of right half of propodeum of female showing lamella (Fig. 12) (× 65); subventral view of genitalia of male (Fig. 13) (× 100).

5–6.x.1988 (F. W. and S. K. Gess), 1 female Paratype and 1 male Paratype; same locality and dates (D. W. Gess), 1 female Paratype and 3 male Paratypes.

Etymology: The name, in the genitive singular, is formed from the generic name, *Wahlenbergia* (Campanulaceae), of the plants in the flowers of which the wasp was commonly found foraging for nectar or nectar and pollen, or near which the wasp was commonly found resting on the ground, and serves to draw attention to the floral association.

Celonites bergenwahliae sp. nov.

Female (Figs 8 and 12)

Black; sometimes portions (especially medially) of a very narrow band along posterior margin of pronotum, sometimes variably developed but always insignificant postero-medial spots on tergites 2–4, *yellowish-white*; distal half of mandibles, whole or portions of a very narrow band along posterior margin of pronotum, whole of tegulae, extreme hind margin of scutellum laterally, middle of metanotum, usually outer portions of propodeal lamellae, most of tergites 1–3 and occasionally part of tergite 4, whole of sternite 1, most of sternite 2, postero-lateral corners of sternite 3, extreme distal ends of femora and whole of tibiae and tarsi of all legs, *reddish-brown*.

Wings lightly browned.

Length 7,5–8,2 mm; length of fore wing 5,0–5,3 mm; hamuli 7.

Head (Fig. 8) with puncturation of frons moderate and fairly close on a finely longitudinally rugose surface and contrasting with finer but denser puncturation on a more strongly longitudinally rugose surface of clypeus and coarser and denser puncturation on vertex. Pronotum, mesopleura, mesonotum, scutellum and dorso-lateral areas of propodeum coarsely and densely punctured; punctures on upper regions of mesopleura with a tendency to form not very noticeable striae.

Clypeus unmodified, its disc evenly convex and without any indication of a keel; frons with a feeble transverse prominence above antennae.

Scutellum medially convex, strongly raised above level of mesonotum and with a wide crenulate anterior furrow.

Propodeal lamella (Fig. 12) of each side wide, broadly truncate distally, with outer edge gently convex, separated from the median part of the propodeum by an inwardly curving slit ending in a relatively small circular emargination; lateral projection of the ventral margin on each side of the median part of the propodeum with its hind edge not transverse but directed anteriorly at 45 degrees and its point narrowly rounded and projecting across upper part of slit well anterior to level of end of lamella.

Male (Figs 9 and 13)

Colouration similar to that of female, differing most noticeably in the possession of yellowish-white markings on the head and in the greater amount of that colour on the pronotum.

Black; whole of clypeus and labrum, occasionally one or two small spots within each ocular sinus, an antero-medially expanded narrow band along posterior margin of pronotum, occasionally a spot on humeral angles, occasionally small and diffuse postero-medial spots on tergites 2–5 or fewer (sometimes these spots are totally absent), *yellowish-white*; distal half of mandibles, whole of tegulae, extreme hind margin of scutellum laterally, tergite 1 (other than

anterior declivity), usually most of tergite 2, sometimes whole of tergite 3 or sometimes this tergite with only a laterally attenuated postero-medial transverse band (sometimes even this lacking), very occasionally median and lateral patches on tergite 4, extreme distal ends of femora and whole of tibiae and tarsi of all legs, *reddish-brown*.

Length 6,2–7,3 mm; length of fore wing 4,0–4,6 mm; hamuli 6–8.

Structure much like that of female, the differences between the sexes being the same as those given above for *C. wahlenbergiae* sp. nov.

Genitalia (Fig. 13); parameres wide and emarginate at their ends, furnished with long and strong inwardly directed curved hairs; each volsella with a longitudinal band of short strong hairs near inner margin; longitudinal hair bands on right and left volsellae opposing one another and together forming a double longitudinal band.

Material examined: Cape Province: Clanwilliam District, Klein Alexandershoek (32° 20′ 20″ S, 18° 46′ E), 8–13.x.1987 (F. W. and S. K. Gess), 1 female Paratype and 3 male Paratypes (all on ground); same locality, 6.x.1988 (F. W. and S. K. Gess), Holotype female, Allotype male, 1 female Paratype and 6 male Paratypes (all in flowers of *Wahlenbergia* sp. B, Campanulaceae); same locality and date (D. W. Gess), 1 female Paratype and 2 male Paratypes; Clanwilliam District, 5 km W of Clanwilliam, road to Graafwater, 12.x.1987 (F. W. and S. K. Gess), 1 male Paratype (on ground).

Etymology: The name, in the genitive singular, is formed from an anagram of the generic name, *Wahlenbergia* (Campanulaceae), of the plants in the flowers of which the wasp was commonly found foraging for nectar or nectar and pollen, or near which the wasp was commonly found resting on the ground, and serves to draw attention to both the floral association and the present wasp species' close resemblance to *C. wahlenbergiae* sp. nov.

C. bergenwahliae sp. nov. is superficially very similar to *C. wahlenbergiae* sp. nov. but is readily distinguishable in the female by the colour of the pronotum and scutellum (black, not reddish-brown), in both sexes by the puncturation of the frons (moderate and fairly close as in Figs 8 and 9, not fine and very sparse as in Figs 6 and 7) and by the form of the lateral projections of the ventral margin of the median part of the propodeum (Fig 12 as compared with Fig. 10), and in the male by the genitalia (Fig. 13 as compared with Fig.11).

Celonites davidi sp. nov.

Male (Fig. 14)

Black; whole of clypeus, proximal half of labrum (distal half is unpigmented and translucent), spot on proximal half of mandibles, large median patch on frons above clypeus, patch entirely filling ocular sinus and extending upwards and downwards along portion of inner eye margin and mesad towards median frontal patch (but not meeting the latter), most of pronotum, narrow elongate marking margining anterior edge of mesopleura opposite pronotal lobes, a spot on tegulae anteriorly, a small spot on antero-lateral corners of scutellum opposite tegular ends, greater part of upper and lower faces of propodeal lamellae, postero-medial spots on tergites 1–6, elongate wedge-shaped postero-lateral markings on tergites 1–3, small spots on distal end of fore femora and proximal end of fore tibiae, *yellowish-white*; antennae (other than for 3 basal segments), distal half of mandibles, pronotal lobe and oblique longitudinal band on each side of pronotum, most of underside of pronotum, most of tegulae, most of scutellum,

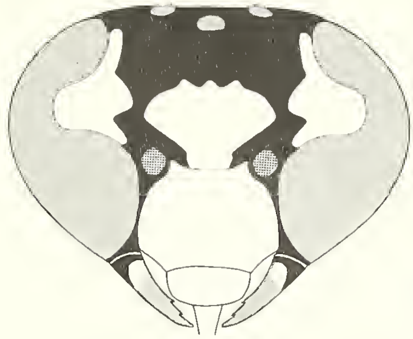


Fig. 14. *Celonites davidi* sp. nov.: frontal view of head of male to show colour pattern (× 25).

median part of metanotum, tergites (other than for above indicated pale markings), most of sternite 2 and parts of sternite 3 laterally, distal part of femora and whole of tibiae (other than for pale spots on fore legs) and tarsomeres 1–4 , *reddish-brown*; coxae, trochanters, proximal part of femora and fifth tarsomeres, sternites (other than indicated above), *dark brown*.

Wings very lightly browned.

Length 6,5 mm; length of fore wing 3,8 mm; hamuli 6.

Head with surface of clypeus, frons and vertex shagreened, with puncturation of frons limited to area immediately adjacent to anterior ocellus where sparse and with that of vertex somewhat coarser and denser. Clypeus and frons unmodified, without any indication of keels.

Thorax and abdomen moderately to coarsely punctured; punctures weakest and least dense on pronotum, most pronounced and densest on mesonotum; punctures on scutellum and upper regions of mesopleura forming weak and very strong longitudinal striae respectively.

Propodeal lamella of each side wide, broadly truncate distally, with outer edge gently curved, separated from median part of propodeum by an inwardly curved slit ending in a relatively large circular emargination; lateral projection of ventral margin on each side of the median part of the propodeum with its hind edge transverse and its point bluntly rounded, wider than long, and projecting across opening of curved slit at level of end of lamella.

Abdominal tergites with posterior outer angles only moderately projecting; tergite 7 with hind margin gently curved and with small lateral emarginations.

Female unknown.

Material examined: Cape Province: Namaqualand, Anenous (29° 14′ 30″ S, 17° 34′ 45″ E), 11–13.x.1988 (D. W. Gess), Holotype male (on ground).

Etymology: The name, in the genitive singular, is formed from the name of the collector of the present specimen, Mr David W. Gess, in recognition of his enthusiastic and discriminating collecting over the years.

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REFERENCE

Richards, O. W. 1962. *A revisional study of the Masarid wasps (Hymenoptera, Vespoidea)*. London: British Museum (Natural History).

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Flower visiting by masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae)

by

SARAH K. GESS and **F. W. GESS**

(Albany Museum, Grahamstown)

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ABSTRACT

Flower visiting records are given for 69 species belonging to six of the seven genera of southern African masarid wasps: *Ceramius* (14 spp.), *Jugurtia* (4 spp.), *Masarina* (3 spp.), *Celonites* (8 spp.), *Quartinia* (10 spp.) and *Quartinioides* (30 spp.).

The records, so far assembled, indicate that southern African masarids are most commonly associated with Mesembryanthemaceae (51%) and Compositae (28%), those species visiting flowers of other families such as Campanulaceae (12%), Scrophulariaceae (5%), Leguminosae (Papilionatae) (3%) and Liliaceae (2%) being the exceptions.

It is demonstrated that the majority of species exhibit fidelity to particular families or even genera of plants and that some species, at least, are probably of importance as pollinators to the plants which they visit.

INTRODUCTION

Studies of flower visiting by aculeate Hymenoptera have been concerned in the main with bees. General works on pollination such as Percival (1969), Proctor and Yeo (1973), Faegeri and van der Pijl (1979), Real (1983), and Barth (1985) have few references to flower visiting by aculeate wasps. Most aculeate wasps are, however, regular flower visitors, both adult male and female depending largely on nectar for nourishment. Though adult aculeate wasps are nectar feeders the larvae of the majority of species feed on spiders or insects supplied by their mothers. The Masaridae are exceptional in that the majority of species provision their larvae, bee-like, with pollen and nectar. Furthermore though short tongues are characteristic of the majority of wasps most masarids have long tongues (Figs 1 and 2), some considerably longer than the wasps' length from the frons to the tip of the abdomen, giving them the potential to obtain nectar from a wide range of flower forms including those in which the nectaries are inaccessible to short tongued wasps. They do not, however, get even a passing mention in Percival, Real, and Faegeri and van der Pijl and are mentioned only briefly in Proctor and Yeo (pages 367–368) and Barth (pages 33 and 61). Sufficient pollen, strategically placed is carried externally by masarid wasps to make them potential pollinators. Pollen for provisioning is ingested and is carried mixed with nectar in the crop. Richards (1962) in his world revision of the Masaridae reviewed the literature on flower visiting by these wasps and concluded that "The higher masarids are so closely attached to particular kinds of flowers that the subject cannot be omitted from any serious study of the group though our knowledge is still very incomplete and inaccurate. It may well be possible in the future to relate the structure of some of the genera to that of the flowers they visit and to the methods they use in exploiting them." Since then one such study has been conducted, the subjects of the study being a North American masarid, *Pseudomasaris vespoides* (Cresson), and flowers of the genus *Penstemon* (Scrophulariaceae) (Torchio, 1974). It has been stated in "A preliminary synthesis of pollination biology in the Cape flora" that Masaridae "are probably important floral visitors in southern Africa" (Whitehead, Giliomee and Rebelo in Rebelo, 1987), however, no indication is given of masarid/flower associations. The present authors have, during the past two decades, in the course of their studies of aculeate wasps and bees in the Cape Floral Region (more especially in the karroid areas of this region), kept records of flower visiting by wasps and bees (Gess and Gess, *Catalogue of flower visits by aculeate wasps*, unpublished). Some of these records have been published, those concerned with Masaridae being in Gess (1968, 1973 and 1981) and in Gess and Gess (1980, 1986, 1988a and 1988b). In the light of the current interest in pollination it seems useful to gather together all the available records of flower visiting by masarid wasps in southern Africa and those as yet unpublished and to assess the degree of fidelity exhibited by these wasps and their possible effectiveness as pollinators.

The family Masaridae (*sensu* Richards, 1962) is constituted of three sub-families, the Euparagiinae, Gayellinae and Masarinae. All three sub-families are represented in the New World but only the Masarinae are represented in the Old World. It is, however, in the Old World and in southern Africa in particular that the greatest speciation has occurred. Seven genera, *Ceramius* Latreille, *Jugurtia* Saussure, *Masarina* Richards, *Celonites* Latreille, *Quartinia* Ed. André, *Quartinioides* Richards and *Quartiniella* Schulthess are represented in southern Africa. *Masarina*, *Quartinioides* and *Quartiniella* are endemic to this region.

In the following account the genera are considered in order of decreasing body length which is associated with increasing relative tongue length (Table 1) (*Quartinia* and *Quartiniella* being the notable exceptions) and not following a systematic or phylogenetic sequence.

The flower visiting records are presented in tabular form necessitating the use of abbreviations. These are:

Colours:	B – blue; O – orange; Pi – pink; Pu – purple; PuPi – purplish pink; V – violet; W – white; Y – yellow; WY – cream.
Sex:	F – female; M – male.
Numbers:	digits – represent numbers of **specimens captured**; m – represents **many observations** of visits to flowers; p – pollen from **provision** representing an **unknown number of visits to flowers**.
Collectors:	CDM – C. D. Michener; CFJG – C. F. Jacot Guillarmod; DWG – D. W. Gess; EMCC – E. McC. Callan; FWG – F. W. Gess; HWG – H. W. Gess; JGHL – J. G. H. Londt; MS – M. Struck; OWR – O. W. Richards; RET – R. E. Turner; RWG – R. W. Gess; SKG – S. K. Gess; WHRG – W. H. R. Gess.

In order to be consistent with earlier papers on Masaridae by Gess and Gess the names Compositae and Leguminosae are used rather than the presently favoured alternative names Asteraceae and Fabaceae. It should be noted that the plant here referred to as *Aspalathus spinescens* Thunb. *lepida* (E. Mey.) Dahlgren (det. J. Vlok, confirmed E. Brink) was previously referred to as *Aspalathus desertorum* Bol. (det. E. Brink following Bayliss BRI 618) (Gess and Gess, 1986, 1988a and 1988b).

Although full locality details are recorded on most specimen labels the localities are given in the tables by district, expressed as the name of the nearest town, as it is more informative for the purposes of this publication to group the localities.

FLOWER VISITING RECORDS

Ceramius Latreille

The genus *Ceramius* occurs in two widely separated geographical regions in the Old World, one being the extreme south west of the Afrotropical Region and the other that portion of the Palaearctic bordering on the Mediterranean Sea. In the Afrotropical Region the genus is in the main restricted to the Cape Province where it is found in Namaqualand, the South Western Cape, the Little Karoo, the southern parts of the Great Karoo and in the Eastern Cape as far east as the Great Fish River. Outside the Cape Province, one species, *C. damarinus* Turner, is endemic to the Kaokoveld and Ovamboland in Namibia (S. W. A.), and one Eastern Cape species, *C. capicola* Brauns, has been recorded from two localities (Kroonstad and Thaba Nchu) in the Orange Free State. The areas favoured by these wasps are in the main characterised by a predominantly winter rainfall and low, semi-arid vegetation. In southern Africa *Ceramius* favours those parts of the Karroid and False Karroid areas (Acocks, 1953 and 1975) which lie within the winter rainfall and spring/autumn rainfall regions. That is those karroid areas which fall within the Cape Floral Region (*sensu* Bond and Goldblatt, 1984) as defined in Rebelo (1987). The flight period in southern Africa is from September to March, the period for individual species being somewhat more limited.

The genus *Ceramius* has been divided on morphological characters into eight species groups (Richards, 1962; Gess and Gess, 1986) one of which has recently been sub-divided (Gess and

Fig. 1. *Ceramius clypeatus* Richards, an example of a relatively short tongued masarid wasp. Above: dorsal view of head with tongue extended (× 14). Below: short length of tongue (glossa) with the two halves separated (× 500).

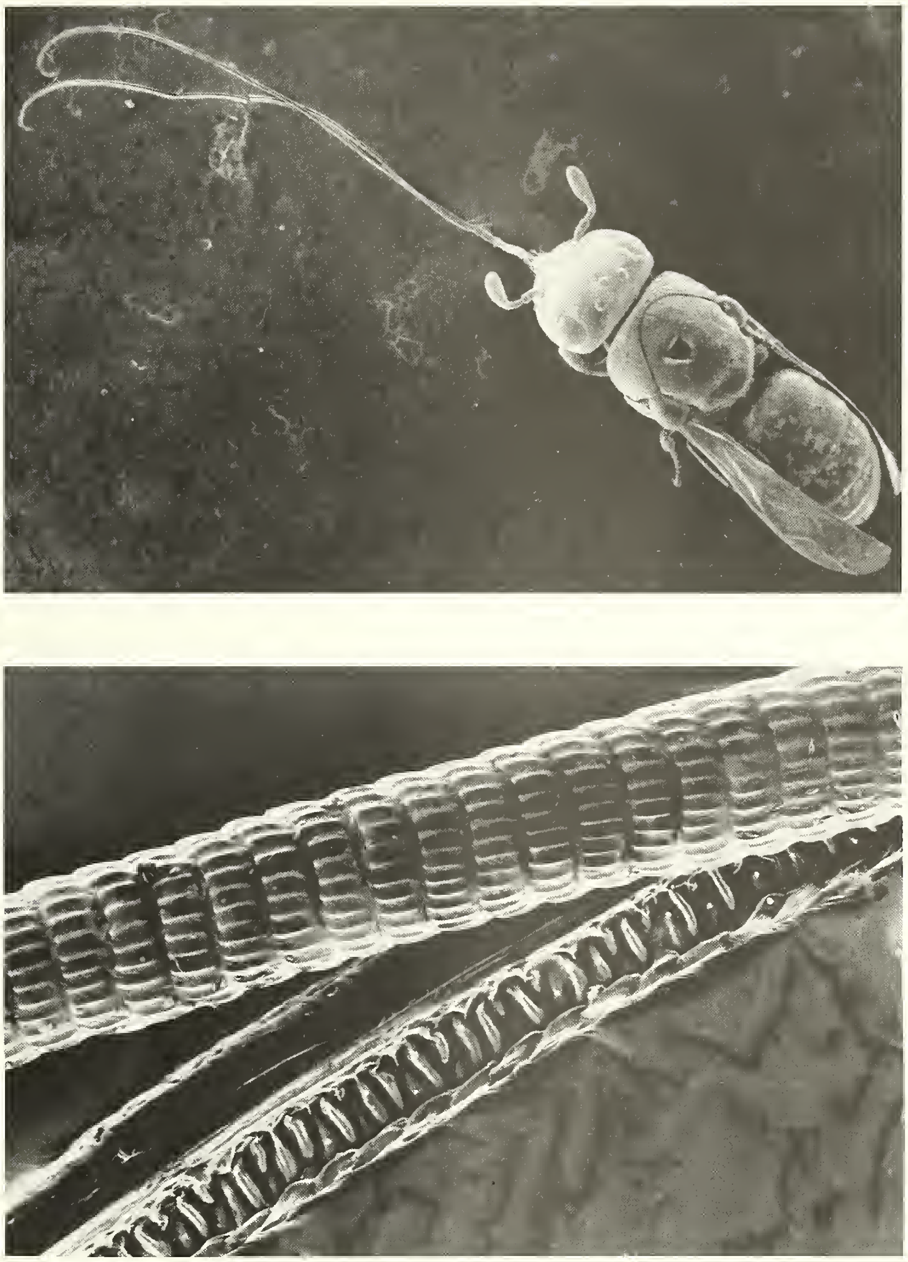

Fig. 2. *Quartinioides laeta* (Schulthess), an example of a relatively long tongued masarid wasp. Above: dorsal view with tongue extended (× 14). Below: short length of tongue (glossa) with the two halves separated (× 500).

Gess, 1988b). Six of these species groups are represented in southern Africa. Compared with other southern African masarids *Ceramius* spp. are medium to large wasps, females ranging in length from 11 mm (*C. bicolor* (Thunb.)) to 22 mm (*C. rex* Saussure). *Ceramius* species are relatively short tongued for masarid wasps (Table 1 and Fig. 1).

TABLE 1.

Body length, tongue length, and tongue length : body length for some southern African masarids.

GENUS	SPECIES	SEX	N	AVERAGE BODY LENGTH mm	AVERAGE TONGUE LENGTH mm	AVERAGE TONGUE LENGTH / AVERAGE BODY LENGTH
Ceramius Latreille						
	bicolor (Thunberg)	F	4	10,83	2,96	0,27
		M	2	10,50	2,92	0,28
	braunsi Turner	F	10	17,28	4,70	0,27
	capicola Brauns	F	8	10,90	2,54	0,23
	clypeatus Richards	F	10	15,43	2,98	0,19
		M	10	15,48	3,18	0,21
	lichtensteinii (Klug)	F	6	17,78	5,56	0,31
		M	4	17,83	5,54	0,31
	nigripennis Saussure	F	6	14,86	4,08	0,27
	rex Saussure	F	1	20,86	5,83	0,28
Jugurtia Saussure						
	braunsi (Schulthess)	F	8	9,92	3,69	0,37
	braunsiella (Schulthess)	F	3	11,17	4,11	0,37
	confusa Richards	F	4	10,17	4,00	0,39
		M	4	10,08	4,23	0,42
Masarina Richards						
	familiaris Richards	F	8	10,09	3,54	0,35
		M	5	8,80	3,28	0,37
	mixta Richards	F	10	8,85	3,71	0,42
		M	8	7,45	2,92	0,39
Celonites Latreille						
	capensis Brauns	F	7	8,89	5,71	0,64
		M	2	8,75	5,04	0,58
	clypeatus Brauns	F	10	8,80	5,68	0,66
		M	2	7,63	4,96	0,65
	peliostomi Gess	F	20	6,76	4,73	0,70
		M	4	7,08	4,17	0,59
	wahlenbergiae Gess	F	6	7,47	4,29	0,57
		M	6	6,88	3,40	0,49
	bergenwahliae Gess	F	3	7,56	4,28	0,57
		M	7	6,56	3,35	0,51
Quartinia Ed. André						
	parcepunctata Richards	F	1	5,53	2,25	0,42
Quartinioides Richards						
	laeta (Schulthess)	F	3	3,69	4,88	1,32
	sp. F	F	2	3,94	5,40	1,37
	sp. M	F	1	4,20	1,76	0,42

Nesting is in burrows excavated with the aid of water in non-friable soil in horizontal or sloping but not vertical ground. As these wasps tend to nest in close proximity to their natal nests

they form nesting aggregations. These aggregations may themselves be extensive or may though small be abundant within an area so that where these wasps occur in large numbers there may be several thousand nests in close proximity (Gess and Gess, 1988b). The burrows are multicellular and are surmounted by a mud entrance turret (Gess and Gess, 1980, 1986 and 1988b). Each larva is provisioned with pollen and nectar presented in the form of a single firm loaf. Pairing at water seems to be most common for *Ceramius* species, however, *C. clypeatus* which has never been observed at water has been observed to pair on the forage plant, the male descending on a foraging female.

The only flower visiting records for Palaearctic *Ceramius* species seem to be few and casual and do not indicate any particular preferences (Richards, 1962 and 1963). Flower visiting records for Afrotropical *Ceramius* species, that is for *Ceramius* species in southern Africa, are listed in Table 2.

It should be noted that records in which digits are given in the column "number" are derived from samples of insects collected and are therefore in no way indicative of numbers of observed instances. This is particularly relevant in the cases of *C. capicola* Brauns, *C. linearis* Klug, and *C. lichtensteinii* (Klug) which, being species very familiar to the authors and common in the Grahamstown district, have been regularly observed by them foraging on "mesems" in large numbers. Similarly the sight of *C. lichtensteinii* foraging in large numbers on *Sphalmanthus cf. bijliae* (N.E.Br.) L.Bol. at Tierberg in the Prince Albert district in December 1987 was noted with interest but only a small number of voucher specimens was collected. *C. bicolor* (Thunberg), *C. clypeatus* Richards, *C. socius* Turner and *C. jacoti* Richards have similarly been observed foraging in greater numbers than the numbers of specimens collected would indicate. Such observations of large numbers of individuals visiting particular flowers are indicated in Table 2 by an "m" in the "numbers" column.

The results of analyses of pollen from pollen loaves, by comparing pollen obtained from these loaves with that from flowers growing in the vicinity of the nests, have been included in Table 2 and are indicated as visits to flowers of a particular species by a female but instead of a digit in the column "number" there is a "p" indicating "provision". In the cases of *C. clypeatus* Richards and *C. braunsi* Turner for which nests have not been found the pollen analysed was taken from the crops of female wasps. These records are also indicated in Table 2 by a "p" in the column "number". Apart from indicating fidelity in flower visiting for the purpose of collecting pollen for provisioning the pollen analyses serve to supplement and support flower visiting records. This is of particular interest for species such as *C. rex* Saussure and *C. nigripennis* Saussure for which flower visiting records are very few and for *C. braunsi* which has been recorded from forage plants of two families.

The records demonstrate that species and species groups within the genus *Ceramius* exhibit marked fidelity to flowers of a single family indicating that pollen and nectar are being obtained from the same plants. A possible exception is *C. braunsi* which has been recorded from both composite flowers and the flowers of *Aspalathus spinescens* Thunb. subsp. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae). Pollen from the crop of a female captured on *Aspalathus* flowers was found to be entirely composite, indicating a fidelity to Compositae when pollen gathering. Visits to *Aspalathus* flowers seem to have been solely for obtaining nectar. Records are too few to establish whether visits to flowers other than composites for obtaining nectar are habitual for *C. braunsi*. There are occasional records of casual visiting of flowers of another family by *C. lichtensteinii* (Group 5) which has been collected on *Blepharis*

(Acanthaceae) and *Senecio pterophorus* (Compositae) and by *C. capicola* (Group 8) which has been collected on *Berkheya* sp. (Compositae). However, pollen from pollen loaves of eight *Ceramius* species, *C. nigripennis* Saussure, *C. jacoti* Richards, *C. lichtensteinii* (Klug), *C. rex* Saussure, *C. bicolor* (Thunberg), *C. socius* Turner, *C. linearis* Klug and *C. capicola* Brauns, and from the crop of one species, *C. clypeatus* Richards, has never been found to contain pollen from mixed families (Gess and Gess, 1980, 1986, 1988b and present paper: Table 2). It is therefore considered that "mesems" are the habitual forage plants of *C. lichtensteinii* and *C. capicola* and that visits to other plants are casual in nature. This opinion is in keeping with that expressed by Cooper (1952) in a consideration of the records of flower visiting by *Pseudomasaris* in North America.

The flower visiting pattern of southern African *Ceramius* derived from the records at present available is:

Group 2a — Mesembryanthemaceae;
Group 2b — Leguminosae: Papilionatae;
Group 3 — Compositae;
Group 4 — Mesembryanthemaceae;
Group 5 — Mesembryanthemaceae;
Group 6 — Compositae;
Group 8 — Mesembryanthemaceae.

Gess (1965) when discussing the distribution of the genus *Ceramius* in southern Africa, at a time when no flower visiting records were available, stated that "it is likely that the flowers visited by *Ceramius* will prove to be low-growing Compositae and mesembryanthemums (Aizoaceae) which following the winter rains, are such a striking feature of the semi-desert areas inhabited by *Ceramius* in South Africa." This prediction has been upheld for the species occurring in karroid areas, of the 14 species for which records are available eight species are associated with Mesembryanthemaceae and five with Compositae. The exception, *C. clypeatus*, which forages on *Aspalathus* seems to be associated with Macchia (Fynbos) (Acocks, 1953 and 1975), more particularly Dry Mountain Fynbos and Mesic Mountain Fynbos (Moll *et al.*, 1984). It is notable that the "mesems" favoured by *Ceramius* species are most commonly white, pink or cream coloured. Dark pink to cerise, red and yellow "mesems" do not seem to be favoured. It is also of note that the composite flowers favoured by *Ceramius* species most commonly have entirely yellow or orange flower heads.

The posture of the wasp when gathering pollen or nectar on a "mesem" flower or a composite capitulum is to a large degree dependent on the relative sizes of the flower or capitulum and the wasp visitor. A flower or capitulum of greater diameter than the length of the wasp may readily be alighted upon (Fig. 3), however, when the diameter of the flower or capitulum is considerably smaller than the length of the wasp a more specialised technique is required. The flower or capitulum is grasped with the second and third pairs of legs and the abdomen is curved down and under to act as a balance.

The pollen gathering method employed by a *Ceramius* species was most clearly determined for *C. braunsi* Turner which was observed during the first week of October 1988 collecting pollen from flowers of *Arctotis laevis* Thunberg and *Athanasia trifurcata* (L.) L. (both Compositae) on a slope above the Clanwilliam Dam. The short curved fore legs were held beneath the wasps as they rotated them one over the other to agitate the anthers and draw the pollen towards the

Fig. 3. *Ceramius braunsi* Turner, collecting pollen, on a capitulum of *Arctotis laevis* Thunberg (Compositae) above the Clanwilliam Dam, October 1988.

mouth for ingestion. The wasp whilst thus engaged receives a coating of pollen on its undersurface (Fig. 4) and this is carried by it to the next capitulum which it visits.

Ceramius clypeatus Richards, when alighting on the small pea flowers of *Aspalathus spinescens* Thunb. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae) grasps the flower with the second and third pairs of legs and curves the abdomen down beneath the flower aiding its balance (Figs 5 and 6). The wasp always holds the alae whilst inserting its tongue at the base of the standard to reach the nectary. Whilst it is thus engaged the carina is forced open and the essential parts curve upwards to make contact with the front legs, which are held folded beneath the wasp, and with the prosternum. A considerable amount of pollen is deposited on these hairy surfaces (Fig. 7) and as the wasp invariably positions itself in this manner it is ideally suited to transfer pollen from one flower to the stigma of another. During the second week of October 1987 and the first week of October 1988 *Ceramius clypeatus* with *Masarina familiaris* Richards (Masaridae) were found to be the commonest insects working the large number of *Aspalathus spinescens lepida* bushes on a hillside above the Clanwilliam Dam. Furthermore their daily period of foraging activity was remarkably long, being from 9.30 am to 5.30 pm. One individual of *C. clypeatus* alone was observed to visit forty flowers in a single foraging excursion.

When collecting pollen for provision *Ceramius clypeatus* grasps the alae with its second and third pair of legs and balances itself in much the same manner as it does when alighting on a flower preparatory to imbibing nectar. It ingests pollen directly from the anthers.

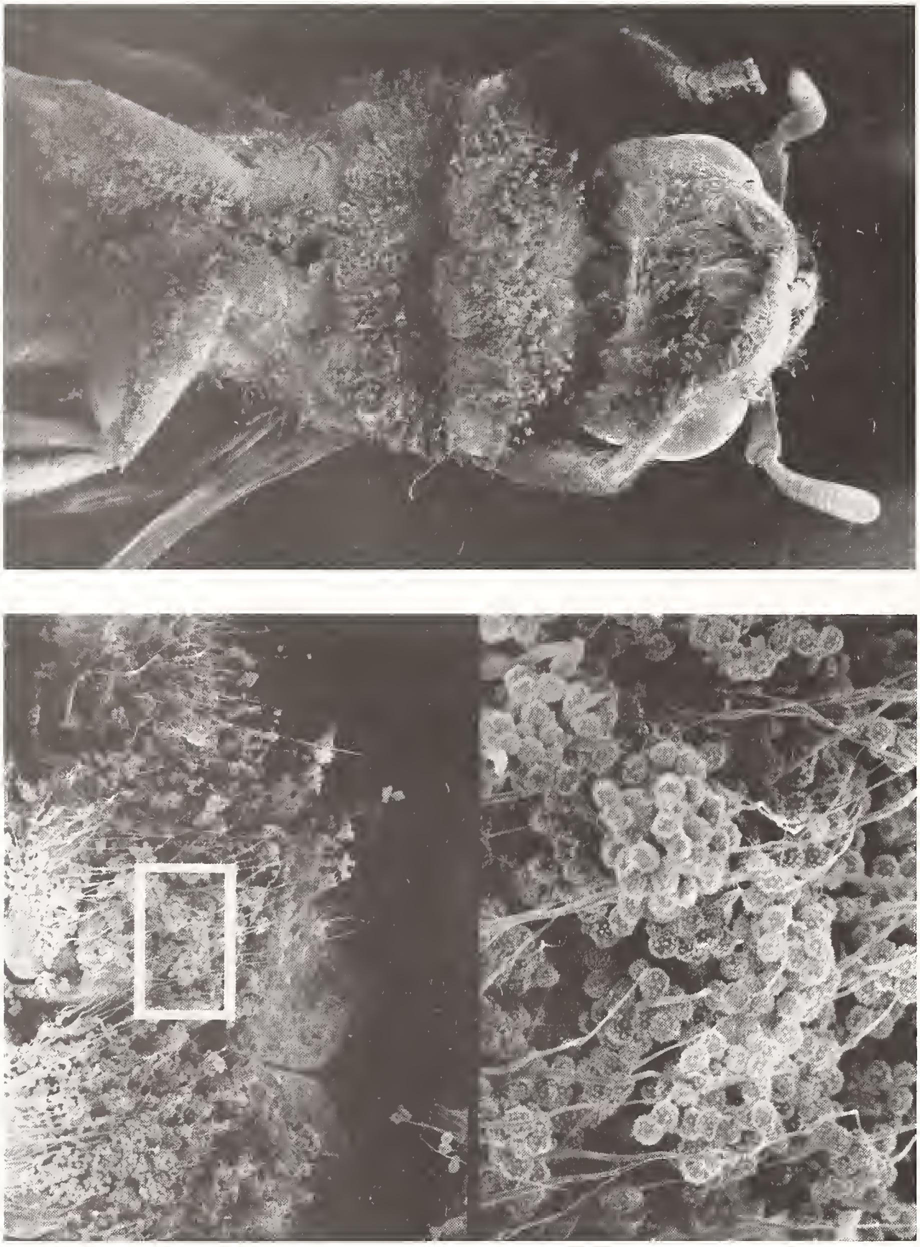

Fig. 4. *Ceramius braunsi* Turner. Above: ventral view of anterior half of wasp showing pollen of *Arctotis laevis* Thunberg (Compositae) on hairy underside (× 11). Below left: part of prosternum and base of front legs (× 30). Below right: boxed area × 150.

Fig. 5. *Ceramius clypeatus* Richards withdrawing from a flower of *Aspalathus spinescens* Thunb. subsp. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae) above the Clanwilliam Dam, October 1988.

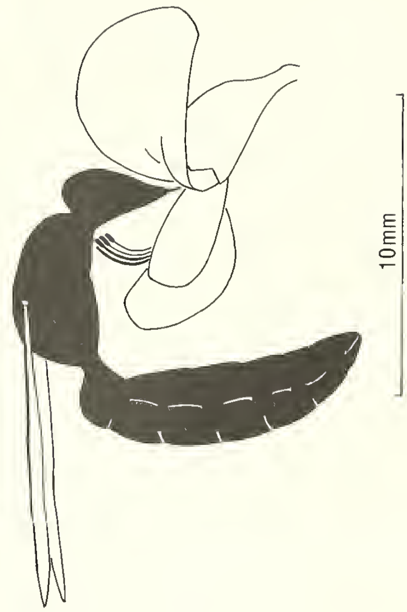

Fig. 6. Simplified diagrammatic representation of *Ceramius clypeatus* Richards (legs omitted) in nectar drinking position on flower of *Aspalathus spinescens* Thunb. subsp. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae).

Table 2.

Flower visiting records for *Ceramius* Latreille in southern Africa.

WASP SPECIES	FORAGE PLANT FAMILY	FORAGE PLANT GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Ceramius Group 2a								
C. cerceriformis Saussure								
	Mesembryanthemaceae							
		Mesembryanthemum sensu lato	Pu	F	1	Garies	FWG&WHRG	7/8.x.85
		Mesembryanthemum L.						
		M. crystallinum L.	W	—	—	Willowmore	CFJG	31.x.67
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	WPi	F	1	Springbok	FWG&SKG	1.x.85
C. peringueyi Brauns								
	Mesembryanthemaceae							
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	WPi	F	14	Vredendal	FWG&SKG	30.ix.85

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Group 2b								
C. clypeatus Richards								
	Leguminosae							
		Aspalathus L.						
		A. spinescens Thunb. subsp. *lepida* (E.Mey) Dahlgren	Y	M	1	Clanwilliam	FWG&SKG	26.ix.85
		A. spinescens Thunb. subsp. *lepida* (E.Mey) Dahlgren	Y	M	1	Clanwilliam	FWG&SKG	28.ix.85
		A. spinescens Thunb. subsp. *lepida* (E.Mey) Dahlgren	Y	F	14	Clanwilliam	FWG&SKG	7–14.x.87
		A. spinescens Thunb. subsp. *lepida* (E.Mey) Dahlgren	Y	F	p	Clanwilliam	SKG	7–14.x.87
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	31	Clanwilliam	FWG&SKG	3–7.x.88
				M	9			
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	2	Clanwilliam	DWG	3–7.x.88
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F&M	m	Clanwilliam	FWG,SKG &DWG	3–7.x.88
Group 3								
C. nigripennis Saussure								
	Compositae							
		Dimorphotheca Vaill. ex. Moench.						
		D. sinuata DC	O	F	2p	Springbok	SKG	9.x.85
		Pentzia Thunb.						
		P. suffruticosa (L.) Hutch. ex. Merxm.	Y	F	1	Springbok	FWG&SKG	15–21.x.87
		Berkheya Ehrh.						
		B. sp.	Y	M	1	Springbok	FWG&SKG	15–21.x.87
		B. fruiticosa (L.) Ehrh.	Y	F	3	Springbok	MS	14–15.x.87
				M	3			
		Hirpicium Cass.						
		H. alienatus (Thunb.) Druce	Y	F	1	Springbok	MS	30.x.87
C. jacoti Richards								
	Compositae							
		Pteronia L.						
		P. incana (Burm.) DC	Y	M	3	Barrydale	CFJG	1.x.67
		Senecio L.						
		S. rosmarinifolius L.f.	Y	F	23	Oudtshoorn	FWG,SKG, HWG&RWG	7–12.xii.85
		S. rosmarinifolius L.f.	Y	F	p	Oudtshoorn	SKG	7–12.xii.87
C. toriger Schulthess								
	Compositae							
		"blue rayed"	B	M	3	Clanwilliam	CDM	19.ix.66
C. braunsi Turner								
	Compositae							
		Athanasia L.						
		A. trifurcata (L.) L.	Y	F	2	Clanwilliam	FWG&SKG	7–13.x.87
		A. trifurcata (L.) L.	Y	F	2	Clanwilliam	FWG&SKG	3–7.x.88
				M	4			
		Arctotis L.						
		A. laevis Thunb.	Y	F	2	Clanwilliam	FWG&SKG	3–7.x.88
		A. laevis Thunb.	Y	F	6	Clanwilliam	DWG	3–7.x.88
		Pentzia Thunb.						
		P. sp	Y	—	1	Clanwilliam	DWG	3–7.x.88
		composite	—	F	p	Clanwilliam	SKG	3–7.x.88

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
	Leguminosae							
		Aspalathus L.						
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	2	Clanwilliam	FWG&SKG	3–7.x.88
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	2	Clanwilliam	DWG	3–7.x.88
				M	1			
Group 4 *C. beyeri* Brauns								
	Mesembryanthemaceae							
		"mesem"	W	F	1	Grahamstown	FWG	16.i.69
		Sphalmanthus N.E.Br.						
		S. cf. bijliae (N.E.Br.) L.Bol.	WPi	F	1	Pr. Albert	FWG, SKG&RWG	26.xi.87–5.xii.87
Group 5 *C. lichtensteinii (Klug)*								
	Mesembryanthemaceae							
		Aridaria N.E.Br.						
		A. sp.	WY	—	—	Grahamstown	FWG&SKG	7.xi.72
		Mesembryanthemum L.						
		M. aitonis Jacq.	W	—	—	Grahamstown	FWG	16.i.69
		Ruschia Schwant.						
		R. sp.	W	—	—	Grahamstown	FWG	11.xii.68
		R. sp.	W	—	—	Grahamstown	FWG	8.i.69
		R. sp.	W	M	1	Grahamstown	FWG	30.xi.70
		R. sp.	PuPi	—	—	Alicedale	FWG	2.xii.70
		R. sp.	PuPi	—	—	Alicedale	JGHL	2.xii.70
		R. sp.	—	F	p	Grahamstown	SKG	
		"mesem"	PuPi	M	1	Grahamstown		29.xi.79
		"mesem"	PuPi	M	1	Grahamstown		26.x.77
		"mesem"	Pi	F	2	Grahamstown	DWG	6.i.81
		"mesem"	W	F	1	Grahamstown	FWG	1.i.81
				M	1		FWG	30.xi.81
		"mesem"	WY	F&M	m	Kommadagga	FWG&SKG	1.xii.85
		"mesem"	W	F&M	m	Kommadagga	FWG&SKG	1.xii.85
		"mesem"	Pi	F&M	m	Kommadagga	FWG&SKG	1.xii.85
		"mesem"	WPi	F&M	m	Grahamstown	FWG&SKG	xii.85-i.86
		Sphalmanthus N.E.Br.						
		S. cf. bijliae (N.E.Br.) L.Bol.	WPi	F	m	Pr. Albert	FWG,SKG &RWG	26.xi.87-5.xii.87
				M	m			
	Compositae (it was noted at the time that there were no mesems in flower)	*Senecio* L.						
		S. pterophorus DC	Y	F	2	Grahamstown		29.xi-2.xii.79
				M	4			
	Acanthaceae							
		Blepharis Juss.						
		B. capensis (L.f.) Pers.	W	F	3	Grahamstown	FWG&DWG	15.i.81
		B. capensis (L.f.) Pers.	W	F	2	Grahamstown	FWG&DWG	3.ii.81
		B. capensis (L.f.) Pers.	W	F	4	Waterford	FWG&RWG	25.xi.87
				M	1			
Group 6 *C. rex* Saussure								
	Compositae							
		Berkheya Ehrh.						
		B. spinosissima (Thunb.) Willd.	Y	F	1	Springbok	FWG	15–21.x.87
		B. spinosissima (Thunb.) Willd.	Y	F	3p	Springbok	SKG	15–21.x.87

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
		"composite" including *B. spinosissima* (Thunb.) Willd.		F	p	Springbok	SKG	15–21.x.87
Group 8								
C. bicolor (Thunberg)								
	Mesembryanthemaceae							
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	WPi	F&M	m	Klawer	FWG&WHRG	14/15.x.65
		P. acutisepalum (Berger) N.E.Br.	WPi	F&M	m	Klawer	FWG&SKG	27.ix.85
		P. acutisepalum (Berger) N.E.Br.	WPi	F	4	Klawer	FWG&SKG	27.ix.85
				M	2			
		P. acutisepalum (Berger) N.E.Br.	WPi	F	p	Klawer	SKG	29.ix.85
		P. acutisepalum (Berger) N.E.Br.	WPi	F	p	Springbok	SKG	4.x.85
		"mesem"		F	p	Springbok	SKG	4.x.85
		"mesems"	W	—	—	Clanwilliam	CDM	19.ix.66
C. socius Turner								
	Mesembryanthemaceae							
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	WPi	F&M	m	Clanwilliam	FWG&SKG	28.ix.85
		"mesem"	W	F	4	Montagu	FWG	3.xii.86
		"mesem"	W	F	2	Montagu	RWG	3.xii.86
		"mesem"	W	F	1	Montagu	SKG	3.xii.86
		"mesem"	W	F	2	Touws River	FWG	4.xii.86
		"mesem"	W	F	5	Montagu	FWG&SKG	4.xii.86
		P. acutisepalum (Berger) N.E.Br.	WPi	F&M	m	Clanwilliam	FWG&SKG	7–14.x.87
		P. acutisepalum (Berger) N.E.Br.		F	p	Clanwilliam	SKG	7–14.x.87
C. linearis Klug								
	Mesembryanthemaceae							
		Aridaria N.E.Br.						
		A. sp.	YW	F	11	Grahamstown	FWG&SKG	17.x.72
				M	10			
		A. dyeri L.Bol.	YW	F	3	Alicedale	FWG	2.xii.70
				M	5			
		A. plenifolia (N.E.Br.) Stearn	YW	F	4	Alicedale	JGHL	2.xii.70
				M	4			
		A. plenifolia (N.E.Br.) Stearn	YW	F	1	Alicedale	FWG	16.xii.71
				M	1			
		Malephora N.E.Br.						
		M. sp.	YW	F	22	Grahamstown	FWG&SKG	26.x.72
				M	44			
		Mesembryanthemum L.						
		M. aitonis Jacq.	W	F	4	Grahamstown	FWG	30.xii.71
				M	3			
		M. aitonis Jacq.	W	F	1	Grahamstown	FWG	28.xi.82
		Ruschia Schwant.						
		R. sp.	PuPi	—	—	Alicedale	JGHL	2.xii.70
		R. sp.	W	—	—	Grahamstown	JGHL	5.xii.69
		Drosanthemum Schwant.						
		D. floribundum (Hw.) Schwant.	Pi	M	1	Grahamstown		29.xi.76

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
		D. floribundum (Hw.) Schwant.			p	Grahamstown	SKG	10.xii.74
		"mesem"	W	F	1	Grahamstown	FWG	13.i.81
		"mesem"	W	M	2	Grahamstown	FWG	30.xi.81
		"mesem"	Y	F	2	Grahamstown	FWG&SKG	22.x.81
				M	1			
		"mesems"		F&M	m	Grahamstown	FWG&SKG	
		"mesem"	YW	F&M	—	Kommadagga	FWG&SKG	1.xii.85
		"mesem"	W	—	—	Kommadagga	FWG&SKG	1.xii.85
		"mesem"	Pi	—	—	Kommadagga	FWG&SKG	1.xii.85
C. capicola Brauns								
	Mesembryanthemaceae							
		Aridaria N.E.Br.						
		A. plenifolia (N.E.Br.) Stearn	YW	—	—	Alicedale	FWG&JGHL	2.xii.70
		Mesembryanthemum L.						
		M. aitonis Jacq.	W	F	—	Grahamstown	FWG	6.ii.69
		Mestoklema N.E.Br.						
		M. tuberosum (L.) N.E.Br.	PuPi	F	—	Grahamstown	FWG	6.ii.69
		M. tuberosum (L.) N.E.Br.	PuPi	F	—	Grahamstown	FWG	18.ii.69
		Ruschia Schwant.						
		R. sp.	W	M	35	Grahamstown	FWG	27.xi.-11.xii.68
		R. sp.	W	F	17	Grahamstown	FWG	8–16.i.69
		R. sp.	W	F	4	Grahamstown	FWG	12.xi.-
				M	15			22.xii.69
		R. sp.	W	M	1	Grahamstown	FWG	30.xi.70
		R. sp.	W	F	8	Grahamstown	FWG	19.xii.71
		R. sp.	W	—	—	Grahamstown	JGHL	4.xii.69
		R. sp.	PuPi	—	—	Alicedale	JGHL	2.xii.70
		Drosanthemum Schwant.						
		D. floribundum (Haw.) Schwant.	Pi	F	p	Grahamstown	SKG	
		"mesems"	—	—	m	Grahamstown	FWG&SKG	
		"mesems"	WY	—	—	Kommadagga	FWG&SKG	1.xii.85
		"mesems"	W	—	—	Kommadagga	FWG&SKG	1.xii.85
		"mesems"	Pi	—	—	Kommadagga	FWG&SKG	1.xii.85
		"mesems"	W	F	4	Hofmeyr	DWG	17.xi.87
				M	5			
	Compositae							
		Berkheya Ehrh.						
		B. sp.	Y	F	1	Thaba Nchu (Orange Free State)	CJFG	1.xii.52

Jugurtia Saussure

Jugurtia is an Old World genus occurring in the Palaearctic Region, bordering the Mediterranean and extending eastwards into Armenia and south western Persia, and in the Afrotropical Region, in Nigeria and southern Africa (Richards, 1962). In southern Africa its distribution parallels that of *Ceramius*. Similarly the flight period in this region is, like that of *Ceramius*, from September to March, the period for individual species being more limited.

Compared with other southern African masarids *Jugurtia* species are medium sized, ranging in length from 7–11 mm. The relative tongue length in *Jugurtia* is greater than in *Ceramius*, however, the actual tongue length is similar (Table 1).

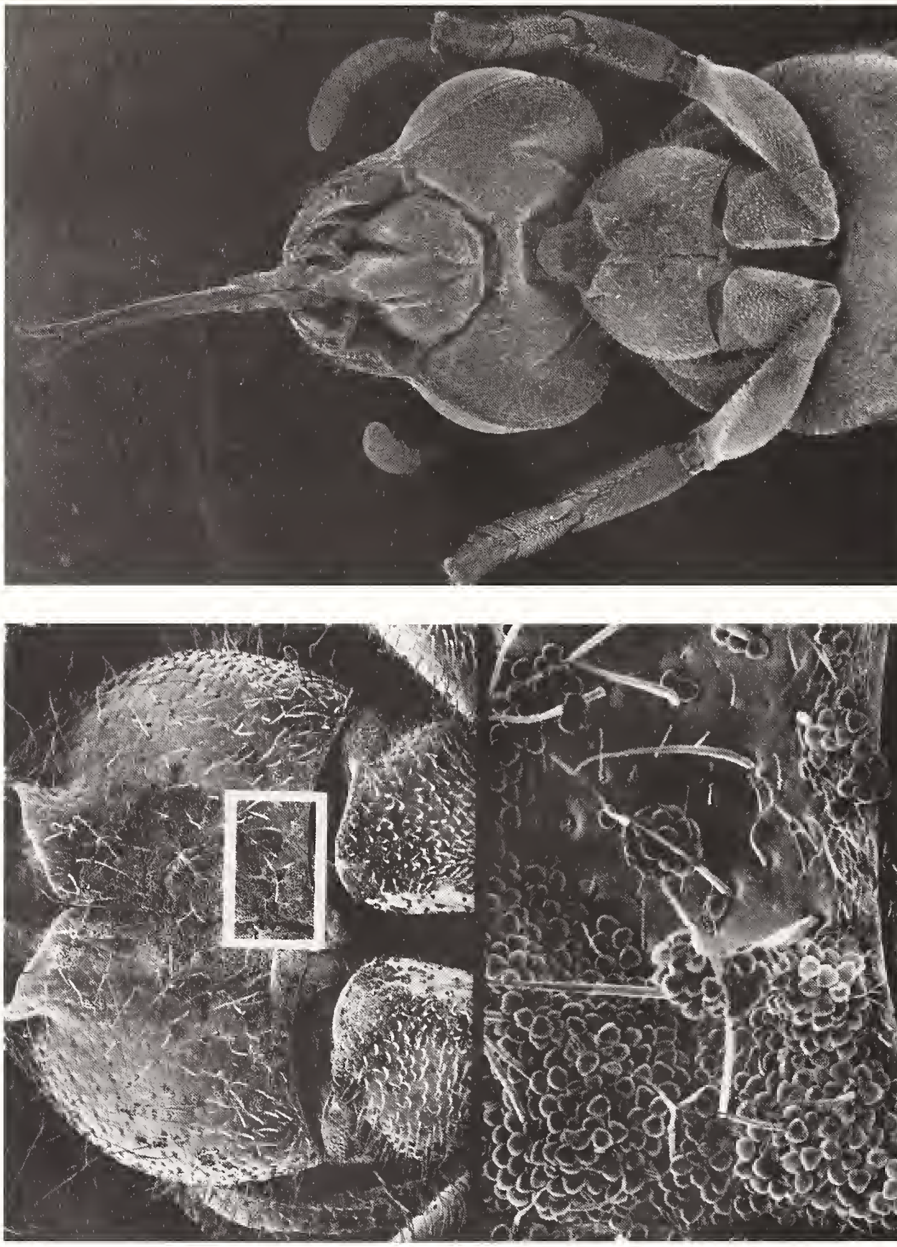

Fig. 7. *Ceramius clypeatus* Richards. Above: ventral view of anterior half of wasp showing area of impact with anthers of *Aspalathus spinescens* Thunb. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae) (× 12). Below left: prosternum and base of front legs (× 30). Below right: boxed area × 150.

Nesting of only one species, *Jugurtia confusa* Richards, has been investigated (Gess and Gess, 1980). This wasp nests in burrows excavated with the aid of water in horizontal ground. Like *Ceramius*, *Jugurtia* forms nesting aggregations. The burrows are multicellular and are surmounted by a mud entrance turret. Each larva is provisioned with pollen and nectar presented in the form of a single loaf.

The only flower visiting records for Palaearctic *Jugurtia* seem to be those of Bequaert (1940 in Richards, 1962) from Algeria. Richards states that "*Jugurtia* as far as the scrappy records go is not attached to any particular family". However, it can be seen from the flower visiting records for *Jugurtia* species from southern Africa listed in Table 3 that preferences similar to those of *Ceramius* are exhibited, Mesembryanthemaceae and Compositae appearing to be favoured. The single record of a male *J. confusa* on *Acacia karroo* may be considered as casual visiting. There is no evidence from pollen loaves examined that this species provisions with any pollen other than that obtained from "mesem" flowers (Gess and Gess, 1980).

The available records are at present too few for it to be possible to note any colour preferences for *Jugurtia* species.

TABLE 3.
Flower visiting records for *Jugurtia* Saussure in southern Africa.

WASP SPECIES	FORAGE PLANT FAMILY	FORAGE PLANT GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
J. confusa Richards								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. parvifolium (Haw.) Schwant.	Pi	F	p	Grahamstown	SKG	8.xii.76
			—	M	1	Grahamstown	—	—
	Leguminosae: Mimosoidea							
		Acacia Mill.						
		A. karroo Hayne.	Y	M	1	Grahamstown	FWG	10.ii.77
J. braunsi (Schulthess)								
	Mesembryanthemaceae							
		"mesem"	Pi	F	1	Springbok	FWG&SKG	1.x. 85
		Drosanthemum Schwant.						
		*D.*sp.	Pi	F	1	Springbok	SKG	15–21.x.87
	Compositae							
		Senecio L.						
		S. sp.	Y	F	4	Springbok	FWG&SKG	10–12.x.88
J. braunsiella (Schulthess)								
	Compositae							
		Lasiospermum Lag.						
		L. bipinnatum (Thunb.) Druce	W	M	1	Grahamstown	FWG&SKG	12.x.77
		Pteronia L.						
		P. paniculata Thunb.	Y	F	1	Grahamstown	FWG&SKG	27.x.72
		Senecio L.						
		S. rosmarinifolius L.f.	Y	F	5	Oudtshoorn	FWG&RWG	7–12.xii.86
		S. rosmarinifolius L.f.	Y	F	p	Oudtshoorn	SKG	
		Felicia Cass.						
		F. sp.	B'	F	1	Springbok	SKG	15–21.ix.87
J. polita Richards								
	Compositae							
		Senecio L.						
		S. sp.	—	M	1	Cradock	OWR (Richards, 1962)	25.ix.52

Masarina **Richards**

The genus *Masarina* is endemic to southern Africa and includes only four described species (Gess and Gess, 1988a). In distribution it seems to be centred in the South Western Cape, only one species, *M. familiaris* Richards, extending to the east as far as Willowmore.

Compared with other southern African masarids *Masarina* species are medium sized, ranging in length from 7,0–11,5 mm. The tongue length is, for masarids, moderate (Table 1).

Nesting is known only for *M. familiaris* (Gess and Gess, 1988a). There seems to be a tendency for an individual wasp to nest in close proximity to her natal nest and therefore for the development of nesting aggregations though at the two nesting sites where the investigations were made the numbers of nests were not great. It is possible that the time of the study, which was opportunistic, was not at the peak nesting period. The nests are burrows excavated with the aid of water in non-friable vertically presented soil. The burrows are multicellular and a downwardly curved mud turret is constructed at the entrance. The provision which is composed of pollen and nectar is moist and sticky and although it forms a single mass it does not form a discrete loaf as does the drier provision of *Ceramius* and *Jugurtia*.

Flower visiting records are available for three species of *Masarina*, *M. familiaris*, *M. mixta* Richards and *M. strucki* Gess. These records are given in Table 4. All the records for *M. familiaris* are for yellow flowered *Aspalathus* species (Leguminosae: Papilionatae). Pollen from the provision of *M. familiaris* was found to be exclusively of the *Aspalathus* type (Gess and Gess, 1988a).

During the second week of October 1987 and the first week of October 1988 *Masarina familiaris* and *Ceramius clypeatus* were found to be the commonest insects working the large number of *Aspalathus spinescens* Thunb. subsp. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae) bushes on a hillside above the Clanwilliam Dam. The daily period of foraging activity was remarkably long, being from 9.30 am to 5.30 pm. This wasp adopts a completely different stance on the small "pea flowers" from that adopted by the larger wasp *C. clypeatus* (Figs 5 and 6). Instead of alighting on the alae it alights on the standard in such a way that it faces downwards towards the centre of the flower (Figs 8 and 9). When imbibing nectar the wasp inserts its tongue into the flower at the base of the standard to reach the nectary causing the carina to open and the essential parts to curve upwards to come firmly into contact with the frons of the wasp (Fig. 9) so that it receives a considerable load of pollen (Fig. 10). As the wasp always positions itself in the same manner it is ideally suited to transfer pollen from one flower to the stigma of another.

When collecting pollen for provision *M. familiaris* ingests it directly from the anthers.

Although *M. familiaris* was observed in abundance on flowers of *Aspalathus* spp. in the second week of October 1987 and the first week of October 1988 and samples of 43 and 57 specimens were taken only one instance of *Masarina mixta* Richards visiting *Aspalathus* flowers was recorded. However, in October 1988 *M. mixta* was found to be a not uncommon visitor to flowers of *Wahlenbergia* sp. A, a sample of 24 specimens having been taken. More records are required, however, a possible preference for *Wahlenbergia* is indicated.

As only one record is available for *M. strucki* no comment can be made.

Fig. 8. *Masarina familiaris* Richards on flower of *Aspalathus spinescens* Thunb. subsp. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae).

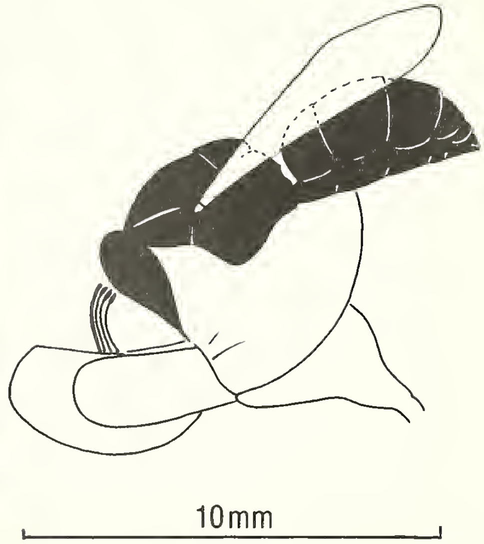

Fig. 9. Simplified diagrammatic representation of *Masarina familiaris* Richards (legs omitted) in nectar drinking position on flower of *Aspalathus spinescens* Thunb. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae).

TABLE 4.

Flower visiting records for *Masarina* Richards in southern Africa.

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COL-OUR	SEX	NUM-BER	LOCALITY	COL-LECTOR	DATE
M. familiaris Richards								
	Leguminosae: Papilionatae							
		Aspalathus L.						
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	22	Clanwilliam	FWG&SKG	8–13.x.87
				M	7			
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	3	Paleisheuvel	FWG&SKG	8–13.x.87
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	43	Clanwilliam	FWG&SKG	3–7.x.88
			M	4				
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	6	Clanwilliam	DWG	3–7.x.88
			M	4				

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F&M	m	Clanwilliam	FWG,SKG &DWG	3–7.x.88
		A. vulnerans Thunb.	Y	F	1	Clanwilliam	FWG&SKG	8–13.x.87
		A. sp.	Y	F	6	Clanwilliam	FWG&SKG	8–13.x.87
				M	4			
		A. sp./spp.		F	p	Clanwilliam	SKG	8–13.x.87
M. mixta Richards								
	Campanulaceae							
		Wahlenbergia						
		W. sp. A	V	F	19	Clanwilliam	DWG	3–7.x.88
				M	4			
		W. sp. A	V	M	1	Clanwilliam	FWG&SKG	3–7.x.88
	Leguminosae: Papilionatae							
		Aspalathus L.						
		A. spinescens Thunb. subsp. *lepida* (E.Mey.) Dahlgren	Y	F	1	Clanwilliam	FWG&SKG	8–13.x.87
M. strucki Gess								
	Sterculiaceae							
		Hermannia L.						
		H. disermifolia Jacq.	—	F	1	Springbok	MS	20.viii.85

Celonites Latreille

Celonites is an Old World genus occurring in the Palaearctic Region in the countries bordering the Mediterranean Sea, northwards to Switzerland and southern Germany and eastwards to Transcaspia and south western Persia, and in the Afrotropical Region in north east Africa and the Cape Province of South Africa (Richards, 1962). In the Cape Province its distribution seems to be similar to that of *Ceramius* and *Jugurtia*: Namaqualand, the South Western Cape, the Little Karoo, the southern parts of the Great Karoo and the Eastern Cape, no further east than the Great Fish River and north to Aliwal North on the Orange River. One species, *C. promontorii* Brauns has been recorded from Thaba Nchu (Orange Free State) (collector C.F.Jacot Guillarmod recorded in Richards, 1962). Collecting records indicate a flight period in the Cape Province of October to December.

Compared with other southern African masarids *Celonites* species are medium sized ranging in length from 7–11,5 mm. The tongue length is relatively long (Table 1).

Little is known concerning the nesting behaviour of *Celonites* due undoubtedly to the cryptic nature of its nests. Brauns (1913) recorded that *Celonites andrei* Brauns constructs fragile mud cells in groups attached to each other lengthwise and situated on the underside of stones and on twigs. Only one group of *Celonites* cells has been discovered by the authors. This group, attached to a stem of a *Peliostomum* plant, consists of three robust mud cells cemented together lengthwise and enclosed in a mud envelope.

Richards (1962) lists flower visiting records for seven Palaearctic species of *Celonites* and one Afrotropical species. He comments that "*Celonites* does not seem to be attached to any one family of plants but nearly all records so far have been made very casually". A few additional records are given in Richards (1969), which might indicate some preference for Labiatae. Flower visiting records for seven southern African species are given in Table 5. Records for *C. capensis* Brauns certainly do not indicate any specificity in flower visiting. Those available for *C. wheeleri*

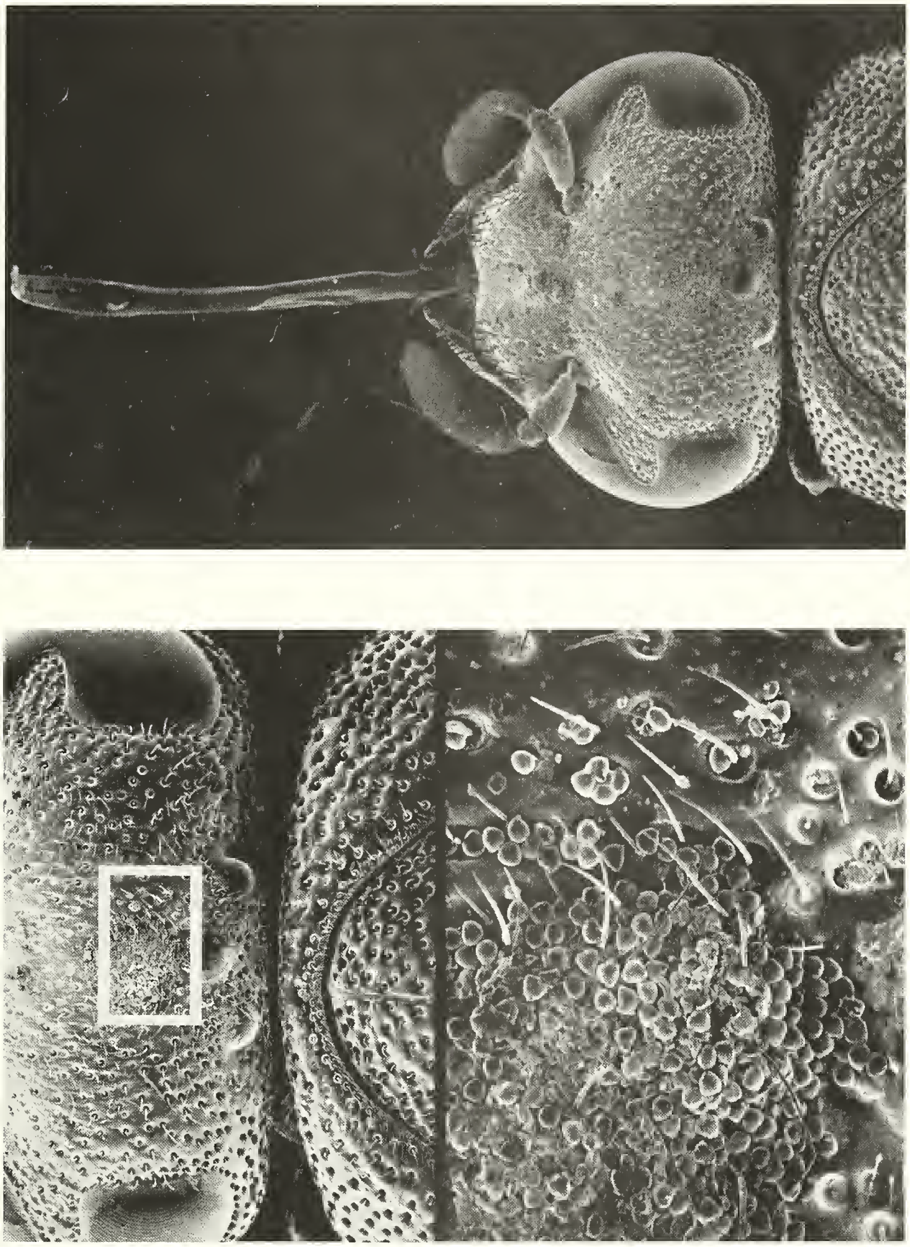

Fig. 10. *Masarina familiaris* Richards. Above: dorsal view of head showing area of impact with anthers of *Aspalathus spinescens* Thunb. *lepida* (E.Mey.) Dahlgren (Leguminosae: Papilionatae) (× 20). Below left: area of impact × 30. Below right: boxed area × 150.

Brauns and C. promontorii Brauns are too few for comment. The sample of specimens of *C. wahlenbergiae* Gess and *C. bergenwahliae* Gess taken from *Wahlenbergia* flowers is small, however, during intensive collecting at various sites in the Clanwilliam district during the periods 8–14.x.1987 and 3–7.x.1988 these wasps were seen to be relatively common in association with flowering *Wahlenbergia* spp. (samples of 28 specimens of *C. wahlenbergiae* and 17 specimens *C. bergenwahliae* were taken) but were found no where else indicating a probable association. Records for *C. andrei* Brauns, *C. clypeatus* Brauns and *C. peliostomi* Gess indicate a clear preference by these species for blue/violet flowers of *Aptosimum* spp. (Scrophulariaceae) (Figs 11 and 12) and the purple/violet flowers of the closely related *Peliostomum virgatum* (Scrophulariaceae) (Figs 13, 14 and 15). Particularly noteworthy is the record of 38 females of *C. peliostomi* collected in flowers of *Peliostomum virgatum* in the Hester Malan Nature Reserve, Springbok (FWG and SKG, 15–21.x.87) and the record of 24+ females of *C. clypeatus* collected in flowers of *Aptosimum depressum* 28 km from Grahamstown (FWG, SKG, DWG and RWG, 13.x.- 3.xii.81). Also of note is the record of the latter species collected in flowers of *Peliostomum virgatum* in the Hester Malan Nature Reserve, showing a constancy of preference between two very widely separated populations.

Flowers of *Aptosimum spinescens* (Thunberg) Weber in the Hester Malan Nature Reserve, Springbok were observed by the authors for an hour, from 10.30–11.30 am on 20.x.87 and visiting insects were recorded. During this period 12 instances of *Celonites* entering flowers were recorded and one instance of an *Anthophora*, which was of too great a diameter to enter these flowers, hovering at the mouth of a flower. A sample of six specimens of *Celonites* was taken as was the *Anthophora*. No other insects approached the flowers. The *Celonites* taken were 5 females of *C. peliostomi* and 1 female of *C. andrei*. On the same day flowers of *Peliostomum virgatum* E.Mey were observed from 12.30–1.15 pm. During this period 22 instances of *Celonites* entering flowers were recorded. No other insects approached the flowers. A sample of 16 specimens was taken. In all during the period 15–21.x.87 a sample of 45 *Celonites* entering flowers of *P. virgatum* was taken. These were 38 female and 3 male *C. peliostomi*, one female *C. andrei* and one female and two male *C. clypeatus*. No other insects were observed in, on or approaching these flowers although they were observed at all times of the day. Flowers of *Aptosimum depressum* in the Grahamstown district observed on various occasions for lengthy periods were found to be visited only by *C. clypeatus* and the very small *Quartinioides tarsata* Richards.

Pollen from the crops and backs of two females of *C.peliostomi*, one from a flower of *A. spinescens* and one from a flower of *P. virgatum* was examined. All the pollen was of the same type and when compared with that from the two flowers was found to match. Similarly pollen from the crop of a female *C. clypeatus* was compared with pollen from *Aptosimum depressum* which it was found to match. These records are indicated in the relevant table with a "p", as were provision records for the other genera.

The flowers of *Aptosimum* species and *Peliostomum* species are gullet flowers (Figs 16 and 17). The corolla is very narrow in the basal region protecting the nectaries from all but minute or long tongued visitors. The greater part of the corolla tube is wider but again restricts the size of visitors wishing to enter the flower. There are four stamens in two pairs, a pair with relatively long filaments and a pair with relatively short filaments. The shorter pair of stamens is sterile in some species of *Aptosimum*. The anthers are adpressed in pairs and positioned dorsally in the flower which has its long axis horizontal. The style lies in a grove dorsally and when fully

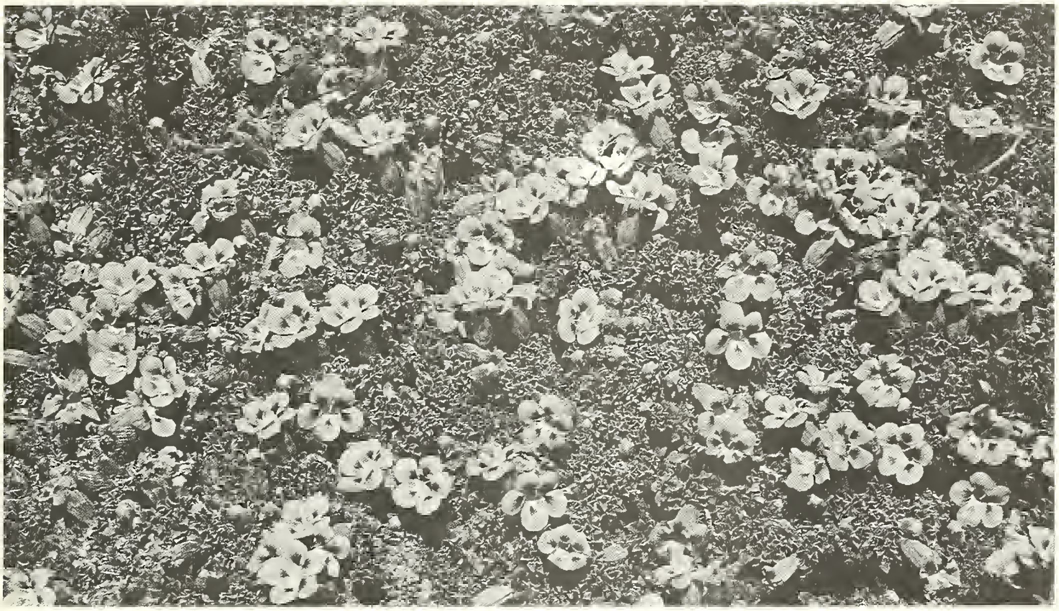

Fig. 11. *Aptosimum depressum* Burch. ex Benth. (Scrophulariaceae).

Fig. 12. *Aptosimum depressum* Burch. ex Benth. (Scrophulariaceae).

Fig. 13. *Peliostomum virgatum* E.Mey. ex Benth. (Scrophulariaceae).

Fig. 14 and 15. *Peliostomum virgatum* E.Mey. ex Benth. (Scrophulariaceae).

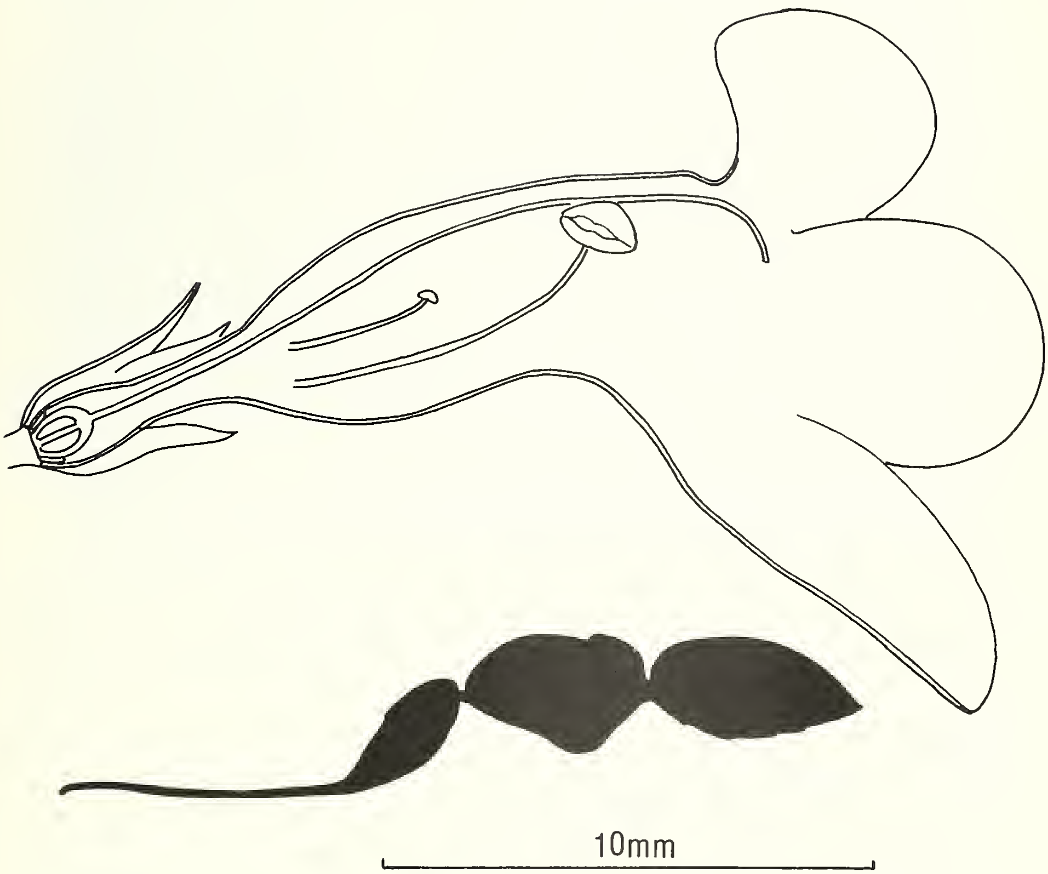

Fig. 16. Simplified diagrammatic representation of longitudinal section of flower of *Aptosimum depressum* Burch. ex Benth. (Scrophulariaceae) and profile of *Celonites clypeatus* Brauns (legs and wings omitted) to demonstrate flower/wasp fit.

extended projects at the mouth of the flower. The tip curves downwards so that the stigmatic surface is downwardly presented.

Celonites spp. when entering these flowers, especially those of *Peliostomum*, fit snugly so that they brush against the stigma and also receive a pollen load, particularly on the hind end of the thorax (Fig. 18). It is even likely that in entering a flower with ripe but not yet dehisced anthers these wasps trigger the dehiscence of the anthers. Having reached the base of the wide portion of the corolla tube they are well able to reach the nectaries. The narrow basal portion

of the corolla tube of *P. virgatum* is 4 mm long, that of *A. spinescens* 4,5 mm long and that of *A. depressum* is 5 mm long. The tongue of *C. peliostomi* which visits *P. virgatum* and *A. spinescens* is 4,8–5 mm long and that of *C. clypeatus* which visits *P. virgatum* and *A. depressum* is 5,8 mm long.

Barth (1985: 61, Fig. 16) gives a short description illustrated with line drawings of the alleged pollen collecting apparatus of *Celonites abbreviatus* (Villers) and the manner in which it is used. The story is ingenious but unfortunately when the authors examined a specimen of *C. abbreviatus* they found that there were no "button-ended collecting bristles on the front surface" of the head. The frons is hairy but the hairs taper towards their tips which are curved.

It seems most likely that as has been observed for *Ceramius* and *Quartinioides* (present paper) and for a pollen ingesting paracolletine bee (Houston, 1981) pollen is simply drawn towards the mouth by the front legs and that it is then ingested. Pollen from dehisced anthers of *Aptosimum* and *Peliostomum* flowers would be freely available for collection from the "floor" of the horizontal corolla tube. Similarly as the flowers of the *Wahlenbergia* spp. visited by *Celonites* spp. are erect pollen from dehisced anthers would be freely available for collection being retained within the cup-like corolla. The description of pollen collecting by *Celonites* in Barth, disregarding the inaccurate description of the hairs, is surely related to grooming behaviour rather than deliberate pollen collection.

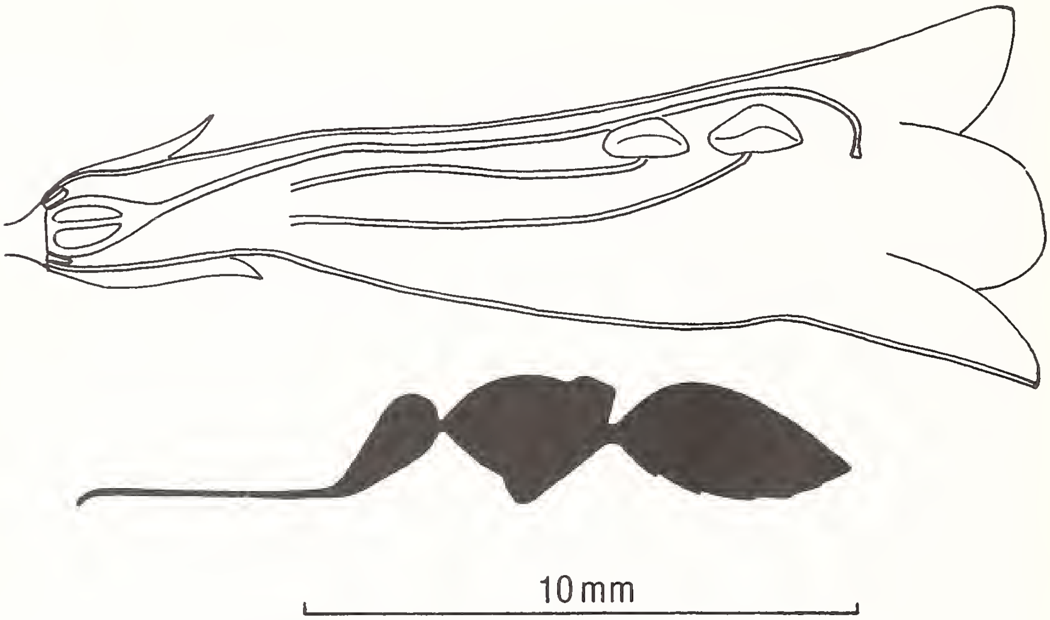

Fig. 17. Simplified diagrammatic representation of longitudinal section of flower of *Peliostomum virgatum* E.Mey. ex Benth. (Scrophulariaceae) and profile of *Celonites peliostomi* Gess (legs and wings omitted) to demonstrate flower/wasp fit.

Fig. 18. *Celonites peliostomi* Gess. Left: dorsal view of posterior end of thorax and anterior end of abdomen showing deposition of pollen (× 30). Right: boxed area × 150.

TABLE 5.

Flower visiting records for *Celonites* Latreille in southern Africa.

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
C. andrei Brauns								
	Scrophulariaceae							
		Aptosimum Burch.						
		A. spinescens (Thunb.) Weber	BV	F	1	Springbok	SKG	15–21.x.87
		Peliostomum Benth.						
		P. virgatum E.Mey ex Benth.	PV	F	1	Springbok	FWG&SKG	15–21.x.87
C. peliostomi Gess								
	Scrophulariaceae							
		Aptosimum Burch.						
		A. spinescens (Thunb.) Weber	PV	F	5	Springbok	FWG&SKG	15–21.x.87
		A. spinescens (Thunb.) Weber	PV	F	p	Springbok	FWG&SKG	15–21.x.87
		A. lineare Marloth & Engl.	BV	M	1	Springbok	SKG	15–21.x.87

WASP SPECIES	FORAGE PLANT FAMILY	FORAGE PLANT GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
		Peliostomum Benth.						
		P. virgatum E.Mey ex Benth.	PV	F	38	Springbok	FWG&SKG	15–21.x.87
				M	3	Springbok	FWG&SKG	15–21.x.87
		P. virgatum E.Mey ex Benth.	PV	F	p	Springbok	FWG&SKG	15–21.x.87
		P. virgatum E.Mey ex Benth.	PV	F	1	Springbok	MS	–.x.1987
C. clypeatus Brauns								
	Scrophulariaceae							
		Aptosimum Burch.						
		A. depressum Burch. ex Benth.	BV	F	24+	Grahamstown	FWG,SKG DWG&RWG	13.x-3.xii.81
		A. depressum Burch. ex Benth.	BV	M	4	Grahamstown	FWG&SKG	22–30.x.81
		A. depressum Burch. ex Benth.	BV	F	p	Grahamstown	FWG&SKG	30.x.81
		Peliostomum Benth.						
		P. virgatum E.Mey ex Benth.	PV	F	1	Springbok	FWG&SKG	15–21.x.87
				M	2	Springbok	SKG	15–21.x.87
C. capensis Brauns								
	Scrophulariaceae							
		Phyllopodium Benth.						
		P. cuneifolium (L.f.) Benth.	BV	F	3	Grahamstown	DWG	9–14.xii.82
	Boraginaceae							
		Ehretia P.Br.						
		E. rigida (Thunb.) Druce	BV	M	1	Grahamstown	FWG&SKG	26.x.77
	Geraniaceae							
		Pelargonium L'Herit.						
		P. myrrhifolium (L.) L'Herit.	WR	F	11	Oudtshoorn	CFJG	10.x.72
				M	1			
	Compositae							
		Berkheya Ehrh.						
		B. sp.	Y	F	4	Riebeek East	FWG	22.xi.82
		B. sp.	Y	F	1	Oudtshoorn	FWG	9–12.xii.86
C. wheeleri Brauns								
	Compositae							
		Berkheya Ehrh.						
		B. cf. spinosa (L.f.) Druce	Y	F	2	Pr. Albert	FWG&SKG	26.xi-5.xii.87
C. promontorii Brauns								
	Compositae							
		Berkheya Ehrh.						
		B. sp.	—	F	4	Thaba Nchu (OFS)	CFJG (Richards, 1962)	1.xi.52
		B. cf. spinosa (L.f.) Druce	Y	F	6	Pr. Albert	SKG	26.xi.-5.xii.87
		Senecio L.						
		S. rosmarinifolius L.f.	Y	F	2	Oudtshoorn	FWG	7–8.xii.86
C. wahlenbergiae Gess								
	Campanulaceae							
		Wahlenbergia Schrad. ex Roth.						
		W. sp. A	V	M	2	Clanwilliam	FWG&SKG	14.x.87
		W. sp. A	V	F	4	Clanwilliam	FWG&SKG	3–7.x.88
		W. sp. A	V	M	3	Clanwilliam	DWG	3–7.x.88

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COL-OUR	SEX	NUM-BER	LOCALITY	COL-LECTOR	DATE
C. bergenwahliae Gess								
	Campanulaceae							
		Wahlenbergia Schrad. ex Roth.						
		W. sp. B	V	F	2	Clanwilliam	FWG&SKG	6.x.88
				M	7	Clanwilliam	FWG&SKG	6.x.88

Quartinia Ed. André

The genus *Quartinia* Ed. André is an Old World genus occurring in the Palaearctic Region bordering the Mediterranean Sea and extending eastwards into Asiatic Russia and India, and in the Afrotropical Region in the South Western Cape, Southern to South Eastern Cape, Namaqualand and Namibia (S. W. A.) (Richards, 1962 and label data, Albany Museum). In numbers it is a relatively large genus.

Compared with other southern African masarids *Quartinia* species are small ranging in length from 2,5–6,5 mm. The tongue is moderately long. It is folded only once on itself as the glossal sac is relatively long.

There are no nesting accounts for *Quartinia*. Of interest, therefore, is the observation that *Quartinia* species have been observed "making burrows in the ground" (C. F. Jacot Guillarmod, pers. com.).

In the Palaearctic Region six species have been collected on Compositae and two species on Chenopodiaceae (Richards, 1962). Flower visiting records for the Afrotropical Region are given in Table 6. Seven of the ten species for which records are available have been recorded from Mesembryanthemaceae only, one species from Aizoaceae, one from Mesembryanthemaceae and Campanulaceae and one from Campanulaceae only. Records of particular interest are those for species which were visiting *Wahlenbergia* spp. (Campanulaceae). Patches of low growing *Wahlenbergia* sp. A at the Clanwilliam Dam were observed for insect visitors during the period 3–7.x.88. The most common visitors were *Quartinia* spp. and *Quartinioides* spp. The plants which were in full flower were approximately 10 cm high. The deep violet flowers which are held erect are 5 mm high with the upper part of the corolla tube 1,6 mm wide and the lower part 0,8 mm wide (Fig. 19). In the bud and the newly opened flower the receptive surfaces of the three stigmatic lobes are closely adpressed to form a knob-like tip to the style. The upper two fifths of the style are hairy particularly at the lower end where the hairs are short and robust and form a distinct collar (Fig. 19a). The anthers dehisce introrsely before the bud opens. When the flower opens the pollen coats the upper part of the style being supported by the collar and giving the whole a club-like appearance. After the flower has been open some little while the hairs supporting the pollen disappear and the pollen falls being retained within the corolla. The style lobes then separate presenting their receptive surfaces (Fig. 19b). The wasps when visiting the flowers alight on the outwardly curved corolla lobes before entering so that when they enter a newly opened flower their dorsal surfaces brush against the pollen clad style and pollen is lodged principally on the hind end of the thorax and the anterior end of the abdomen. When a wasp comes from such a newly opened flower and then enters a flower in which the stigmatic lobes have spread out pollen will be transferred from it to the stigma. *Quartinia* spp. are particularly well suited to effect pollination as they fit the flowers very snugly (Fig. 19c).

TABLE 6.

Flower visiting records for *Quartinia* Ed. André in southern Africa.

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. persephone Richards								
	Mesembryanthemaceae							
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	Pi	F	1	Clanwilliam/ Klaver	FWG&SKG	27.ix.65
	Campanulaceae							
		Wahlenbergia Schrad. ex Roth.						
		W. sp. A	V	F	1	Clanwilliam	DWG	3–7.x.88
		W. sp. D	V	F	1	Clanwilliam	DWG	5–6.x.88
				M	2			
		W. sp. D	V	M	1	Clanwilliam	FWG&SKG	5–6.x.88
Q. parcepunctata Richards								
	Campanulaceae							
		Wahlenbergia Schrad. ex. Roth.						
		W. sp. A	V	F	13	Clanwilliam	DWG	3–7.x.88
				M	1			
		W. sp. A	V	F	5	Clanwilliam	FWG&SKG	3–7.x.88
				M	1			
		W. sp. D	V	F	4	Clanwilliam	FWG&SKG	5–6.x.88
Q. ochraceopicta Schulthess								
	Mesembryanthemaceae							
		"mesem"	W	—	—	Aus (Namibia)	RET	(Turner, 1939)
Q. punctulatum Schulthess								
	Mesembryanthemaceae							
		Mesembryanthemum L.						
		M. crystallinum L.	YW	—	—	Aus (Namibia)	RET	(Turner, 1939)
		M. crystallinum L.	YW	—	—	Matjesfontein	RET	(Turner, 1939)
		M. crystallinum L.	YW	—	—	Pr. Albert Road	RET	(Turner, 1939)
Q. media Schulthess								
	Mesembryanthemaceae							
		Mesembryanthemum	crimson	—	—	Worcester	RET	(Turner, 1939)
Q. vegipunctata Schulthess								
	Mesembryanthemaceae		—	—	—	—	RET	(Turner, 1939)
Q. atra Schulthess								
	Mesembryanthemaceae							
		Mesembryanthemum	—	—	—	—	RET	(Turner, 1939)
Q. sp. A								
	Mesembryanthemaceae							
		Polymita N.E.Br.						
		P. albiflora (L.Bol.) L.Bol.	—	F	1	Springbok	MS	6.xi.87
Q. sp. B								
	Mesembryanthemaceae							
		Prenia N.E.Br.						
		P. sladeniana (L.Bol.) L.Bol.	—	F	1	Springbok	MS	17.x.87

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. jocasta Richards								
	Aizoaceae							
		Galenia L.						
		G. filiformis (Thunb.) N.E.Br.	—	F	2	Springbok	MS	3.xi.87

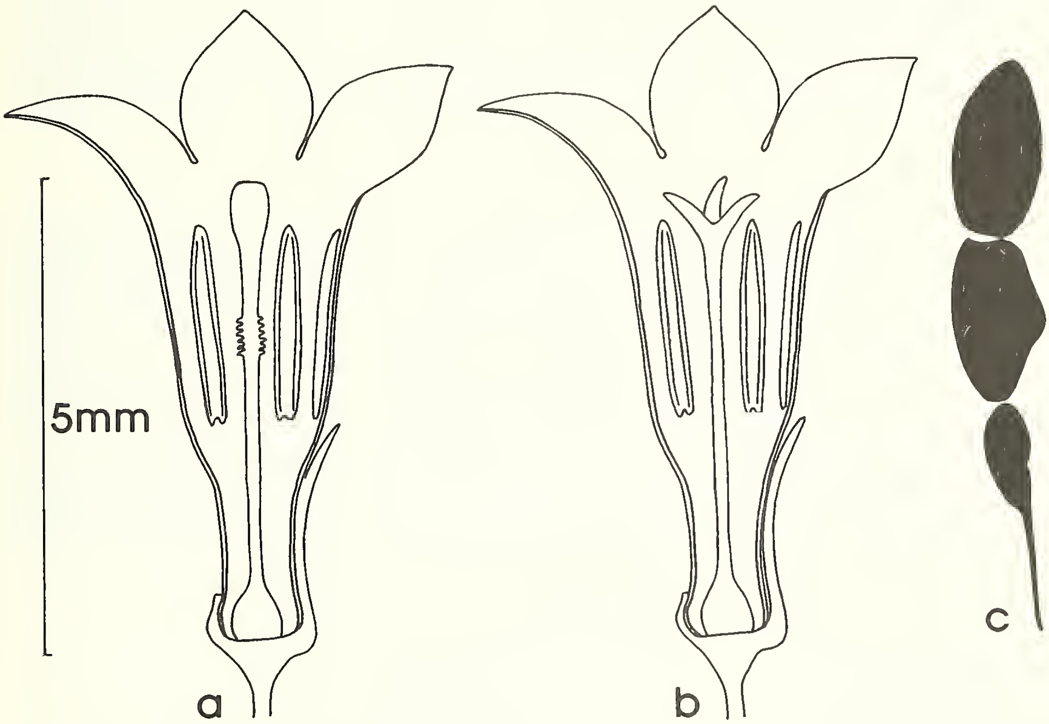

Fig. 19. (a and b). Simplified diagrammatic representations of longitudinal sections of two flowers of *Wahlenbergia* sp. A: (a) freshly opened with stigmatic lobes closely adpressed and pronounced collar of hairs and (b) open for some time with stigmatic lobes separated and collar of hairs withered away. (c). Simplified diagrammatic representation of *Quartinia parcepunctata* Richards (legs and wings omitted) to demonstrate flower/wasp fit.

Quartinioides Richards

The genus *Quartinioides* Richards is endemic to southern Africa where it is recorded from the South Western Cape, the Southern Cape, the Eastern Cape, Namaqualand, Namibia (S. W. A.), Lesotho (Basutoland) and Bulawayo, Zimbabwe (Southern Rhodesia) (Richards, 1962). In numbers of species it is a relatively large genus. Richards (1962) lists 38 species but states that he expects that there are many more species. The species here listed by letter from A–T represent species which could not be determined and must include many undescribed species. Clearly a revision of the genus is required, however, for the present purpose, that of determining the flower visiting pattern of the genus, names are not essential.

Figs 20—22. *Quartinioides* sp. I in flower of *Drosanthemum* sp. (Mesembryanthemaceae) at Anenous, Namaqualand, October 1988.

Figs 23–25. *Quartinioides laeta* (Schulthess) in flower of *Stoeberia* sp. (Mesembryanthemaceae) at Aggeneys, Bushmanland, October 1988.

Figs 26–28. *Quartinioides* sp. M in flower of *Wahlenbergia* sp. C (Campanulaceae) at Anenous, Namaqualand, October 1988.

Compared with other southern African masarids *Quartinioides* species are small, 2,5–5,0 mm in length. The greatest relative tongue length (1,37 × body length) is found in *Quartinioides* (Table 1 and Fig. 2). As the glossal sac is relatively short the tongue when retracted is folded several times upon itself. That not all species of *Quartinioides* have remarkably long tongues is demonstrated by *Q*. sp. M in which the tongue is less than half the body length (Table 1). This remarkable variation in tongue length seems to be related to the nature of the flowers visited, the two remarkably long tongued species listed being visitors to "mesems" and the relatively shorter tongued species being a visitor to *Wahlenbergia*.

There are no nesting accounts for *Quartinioides*. Of interest, therefore is the observation of *Quartinioides* sp. H excavating burrows in sand in the coastal dunes at McDougal Bay near Port Nolloth on the west coast (Gess and Gess, 1985, unpublished field notes). The nests as might be expected were not surmounted by entrance turrets. Pairing on flowers has been observed.

Flower visiting records for 30 species of *Quartinioides* are listed in Table 7. There appears to be, as also noted for *Ceramius* and *Jugurtia*, a marked association between these wasps and flowers of the families Mesembryanthemaceae (18 spp.) (Figs 20–25) and Compositae (7 spp.), favoured colours seeming to be light shades for the Mesembryanthemaceae and yellow to orange for Compositae. Also of interest is a possible preference by some species for *Wahlenbergia* spp. (Campanulaceae) (3 spp.) (Figs 26–28), a preference which is also indicated for some species of *Celonites* (Table 5) and *Quartinia* (Table 6). Of particular interest is the association of *Q. antigone* Richards with *Aloe striata* (Liliaceae), 24 females and 5 males being indicative of more than casual visiting.

When collecting nectar from "mesem" flowers *Quartinioides* insert themselves deeply into the flower being visited, however, when collecting pollen from these and composite capitula they stand on their second and third pairs of legs on the "surface" of the flower or capitulum with the first pair of legs beneath them being rotated in such a manner that the anthers are agitated and the pollen is drawn forwards for ingestion in a similar manner to that observed for *Ceramius braunsi*. When visiting *Wahlenbergia* flowers they alight on the lip of the corolla and then enter. Being smaller than *Quartinia* they are able to turn around in the flower and may therefore emerge head first. Although they do not "fit" the flowers as snugly as *Quartinia*, through their activities in the flowers they probably serve effectively as agents transfering pollen from one flower to the stigma of another.

Quartinioides are generally the commonest visitors to the plants which they patronize and this combined with their usually being very numerous makes them potentially of importance as pollinators to their forage plants.

TABLE 7.

Flower visiting records for *Quartinioides* Richards in southern Africa.

WASP	FORAGE PLANT							
SPECIES	FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. antigone Richards								
	Liliaceae							
		Aloe L.						
		A. striata Haw.	PiO	F	24	Pr. Albert	FWG	26.xi-
				M	5			5.xii.87

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COL-OUR	SEX	NUM-BER	LOCALITY	COLLEC-TOR	DATE
Q. helichrysi Richards								
	Compositae							
		Helichrysum Mill.						
		H. fruticans (L.) D.Don.	—	F	3	Lesotho	CFJG	28.xii.48
		H. fruticans (L.) D.Don.	—	F	5	Lesotho	CFJG (in Richards, 1962)	28–31.xii.48
Q. metallescens (Schulthess)								
	Compositae							
		Gazania Gaertn.						
		*G.*sp.	—	F	1	Lesotho	CFJG	3.xi.48
		G. linearis (Thunb.) Druce	Y	F	2	Lesotho	CFJG	9.xi.48
		Helichrysum Mill.						
		H. sp.	—	F	1	Lesotho	CFJG (in Richards, 1962)	9–17.xi.52
Q. senecionis Richards								
	Compositae							
		Senecio L.						
		S. laevigatus Thunb.	—	F	9	OFS	CFJG	1.xii.52
				M	1			
		S. laevigatus Thunb.	—	F	27	OFS	CFJG	1.xii.52
				M	2		(in Richards, 1962)	
		Aster L.						
		A. muricatus Thunb.	BV	F	6	Lesotho	CFJG	12.xii.54
				M	1			
		A. muricatus Thunb.	BV	F	11	Lesotho	CFJG	12.xii.54
				M	7		(in Richards, 1962)	
		Gazania Gaertn.						
		G. sp.	—	—	—	Lesotho	CFJG (in Richards, 1962)	13.xi.48
Q. poecila (Schulthess)								
	Compositae							
		Berkheya Ehrh.						
		B. sp.	—	—	—	Namibia	RET (Turner, 1939, in Richards, 1962)	
Q. basuto Richards								
	Compositae							
		Gazania Gaertn.						
		G. linearis (Thunb.) Druce	Y	F	1	Lesotho	OWR	29.ix.52
				M	1		(in Richards, 1962)	
		Aster L.						
		A. muricatus Thunb.	BV	F	1	Lesotho	CFJG	17.xi.52
Q. propinqua (Schulthess)								
	Compositae							
		Hirpicium Cass.						
		H. echinus Less.	Y	F	7	Aggeneys	FWG&SKG	14.x.88
Q. sp. G								
	Compositae							
		Berkheya Ehrh.						
		B. cf. spinosa (L.f.) Druce	Y	F	1	Pr. Albert	SKG	26.xi-5.xii.87
Q. sp. I								
	Compositae							
		"daisy"	Y	F	4	Springbok	FWG&SKG	10–12.x.88
	Mesembryanthemaceae							
		Prenia N.E.Br.						
		P. pallens (Ait.) N.E.Br.	—	F	3	Springbok	MS	27.x.87
		Drosanthemum Schwant.						
		D. sp.	Pi	F	3	Anenous	FWG&SKG	11–13.x.88

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. tarsata Richards								
	Mesembryanthemaceae							
		Delosperma N.E.Br.						
		D. acuminatum L.Bol.	—	—	12	Grahamstown	CFJG	24.iv.64
		Drosanthemum Schwant.						
		D. hispidum (L.) Schwant.	Pi	F	2	Grahamstown	EMCC	18.x.52
		D. hispidum (L.) Schwant.	Pi	F	1	Grahamstown	EMCC (in Richards, 1962)	10.x.53
	Scrophulariaceae							
		Aptosimum Burch.						
		A. depressum Burch. ex Benth.	BV	F	14	Grahamstown	FWG&SKG	13–30.x.81
Q. sp. A								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. sp.	Pi	F	1	Bitterfontein/ Garies	SKG	14.x.87
Q. sp. B								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. sp.	Pi	F	1	Bitterfontein/ Garies	SKG	14.x.87
Q. sp. C								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. hispidum (L.) Schwant.	Pi	F	1	Springbok	FWG&SKG	15–21.x.87
Q. laeta (Schulthess)								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. hispidum (L.) Schwant.	Pi	F	1	Springbok	FWG&SKG	15–21.x.87
		Psilocaulon N.E.Br.						
		P. acutisepalum (Berger) N.E.Br.	WPi	—	1	Springbok	FWG&SKG	15–21.x.87
		Stoeberia Dinter & Schwant.						
		S. sp.	Pi	F M	275 10	Aggeneys	FWG&SKG	14.x.88
		S. sp.	Pi	F M	62 25	Aggeneys	DWG	14.x.88
		Prenia N.E.Br.						
		P. sladeniana (L.Bol.) L.Bol.	—	F	1	Springbok	MS	17.x.87
Q. sp. E								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. hispidum (L.) Schwant.	Pi	F M	2 1	Springbok	FWG&SKG	15–21.x.87
Q. sp. F								
	Mesembryanthemaceae							
		Sphalmanthus N.E.Br.						
		S. cf. bijliae (N.E.Br.) L.Bol.	WPi	F M	209 8	Pr. Albert	FWG,SKG &RWG	26.xi-5.xii.87
		Psilocaulon N.E.Br.						
		P. cf. articulatum (Thunb.) Schwant.	Pi	F	19	Pr. Albert	FWG,SKG &RWG	26.xi-5.xii.87

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. sp. H								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. sp.	Pi	F	15	Port Nolloth	FWG&SKG	2.x.85
		D. sp.	Pi	F	1	Port Nolloth	FWG&SKG	11.x.88
		D. sp.	Pi	F	1	Port Nolloth	DWG	11.x.88
Q. sp. K								
	Mesembryanthemaceae							
		"mesem"	YW	F	1	Willowmore	CFJG	4.x.71
Q. sp. J								
	Mesembryanthemaceae							
		"mesem"	Y	F	26	Oudtshoorn	FWG	7–8.xii.86
		"mesem"	Y	F	10	Oudtshoorn	SKG	7–8.xii.86
		"mesem"	Y	M	1	Oudtshoorn	FWG	7–8.xii.86
Q. capensis (Kohl)								
	Mesembryanthemaceae							
		Mesembryanthemum	W	—	—	Cape Town	RET	(Turner, 1939)
			W	—	—	Mossel Bay	RET	(Turner, 1939)
Q. niveopicta (Schulthess)								
	Mesembryanthemaceae							
		Mesembryanthemum	—	—	—	—	RET	(Turner, 1939)
Q. signata (Schulthess)								
	Mesembryanthemaceae							
		Mesembryanthemum	—	—	—	—	RET	(Turner, 1939)
Q. sp. O								
	Mesembryanthemaceae							
		Stoeberia Dinter & Schwant.						
		S. sp.	Pi	F	3	Aggeneys	FWG&SKG	14.x.88
		S. sp.	Pi	F	3	Aggeneys	DWG	14.x.88
		Prenia N.E.Br.						
		P. pallens (Ait.) N.E.Br.	—	F	1	Springbok	MS	27.x.87
		Polymita N.E.Br.						
		P. albiflora (L.Bol.) L.Bol.	—	F	1	Springbok	MS	31.x.87
Q. sp. P								
	Mesembryanthemaceae							
		Prenia N.E.Br.						
		P. pallens (Ait.) N.E.Br.	—	F	4	Springbok	MS	27.x.87
		P. sladeniana (L.Bol.) L.Bol.	—	F	1	Springbok	MS	17.x.87
Q. sp. Q								
	Mesembryanthemaceae							
		Stoeberia Dinter & Schwant.						
		S. sp.	Pi	M	1	Aggeneys	DWG	14.x.88
Q. sp. R								
	Mesembryanthemaceae							
		Stoeberia Dinter & Schwant.						
		S. sp.	Pi	M	1	Aggeneys	DWG	14.x.88
Q. sp. T								
	Mesembryanthemaceae							
		Drosanthemum Schwant.						
		D. sp.	Pi	F	1	Anenous	FWG&SKG	11–13.x.88
Q. sp. M								
	Campanulaceae							
		Wahlenbergia Schrad.						
		W. sp. C	V	F	3	Anenous	FWG&SKG	11–13.x.88
		W. sp. C	V	F	2	Anenous	DWG	11–13.x.88

WASP SPECIES	FORAGE PLANT FAMILY	GENUS AND SPECIES	COLOUR	SEX	NUMBER	LOCALITY	COLLECTOR	DATE
Q. sp. N								
	Campanulaceae							
		Wahlenbergia Schrad.						
		W. sp. A	V	F	5	Clanwilliam	FWG&SKG	3–7.x.88
		W. sp.	V	F	1	Clanwilliam	FWG&SKG	5–6.x.88
Q. sp. S								
	Campanulaceae							
		Wahlenbergia Schrad.						
		W. sp. A	V	M	1	Clanwilliam	DWG	3–7.x.88

***Quartiniella* Schulthess**

The genus *Quartiniella* Schulthess is endemic to southern Africa where it is recorded from the South Western Cape; Southern Cape in the Little Karoo east to Willowmore; and in Namibia (S. W. A.) (Richards, 1962 and label data, Albany Museum). In numbers it appears to be a small genus.

Quartiniella falls within the same size range as *Quartinioides* from which, however, it differs markedly in being relatively short tongued.

Nothing seems to be known of the nesting of *Quartiniella*.

Flower visiting records for *Quartiniella* seem to be almost entirely lacking. According to Turner (1939) two species "are found on *Athanasia* sp. (Compositae) and do not visit *Mesembryanthemum*".

DISCUSSION

Masarid wasps differ from all other wasps in that they depend on flowers not only for nectar for adult nourishment but also for both nectar and pollen for the nourishment of the young. It is therefore important to bear in mind that, though visits by males are solely for imbibing nectar for their own nourishment, visits by females to particular flowers may be for this purpose or to collect nectar and/or pollen for provisioning.

Generally speaking wasps are attracted in large numbers and great diversity to whatever suitable plants may be in flower, extremely popular are plants with small, white, cream or yellow flowers presented in heads. Amongst those plants especially favoured in southern Africa are *Acacia* spp. (Leguminosae: Mimosoidea), *Maytenus* spp. (Celastraceae), *Asclepias* spp. (Asclepiadaceae) and the roadside weed *Foeniculum vulgare* A. W. Hill (Umbelliferae) (Gess and Gess, *Catalogue of flower visits by aculeate wasps*, to date including in excess of 4 000 records for *circa* 420 species, unpublished). It is noteworthy that masarid wasps are almost entirely absent from samples of wasps from such plants.

From the available flower visiting records it appears that southern African masarids as a whole are most commonly associated with Mesembryanthemaceae (51%) and Compositae (28%), those species visiting flowers of other families such as Campanulaceae (12%), Scrophulariaceae (5%), Leguminoseae (Papilionatae) (3%) and Liliaceae (2%) being the exceptions. Furthermore, that individual species on the whole show extreme fidelity to flowers of a single family of plants suggests that both nectar and pollen are generally obtained from the same source. A possible exception is *Ceramius braunsi* which, as already discussed, appears to provision entirely with composite pollen but has been observed taking nectar from *Aspalathus*

flowers. Casual nectar gathering by a species which normally exhibits marked fidelity has been noted for *Ceramius lichtensteinii*.

Clearly the considerable fidelity shown by masarids in their choice of provision is indicative of the importance of particular families or even genera of plants to these wasps. What is more difficult to assess is the importance of the wasps as pollinators to the plants which they visit.

Certainly where masarids are abundant they are probably the commonest and most dependable visitors to certain species of relatively small to medium flowered light coloured "mesems" although bees are not uncommon visitors to these flowers. It is of interest that these "mesem" flowers are not favoured by monkey beetles of the genus *Anisonyx* (Scarabaeidae: Hopliini) which, however, are particularly attracted to "mesem" flowers of the darker shades of purplish pink to magenta, not favoured by masarids. Some at least of the composite flowers visited by masarid wasps are also visited by other insects, non-masarid wasps, bees, flies, beetles and butterflies, which may pollinate these flowers. Generally speaking they are, however, probably less dependable visitors than the masarids where these are abundant. A notable exception is *Fidelia braunsiana* Friese (Hymenoptera: Apoidea: Fideliidae) which is restricted to the genus *Berkheya* (Compositae) (Whitehead, 1984). Certainly the dependence of certain masarid wasps on the flowers of Mesembryanthemaceae and of others on Compositae and the nature of their behaviour in and on these flowers makes them ideally suited to being dependable pollinators.

Evidence is building up to suggest that *Wahlenbergia* spp. are of importance to some species of the smaller masarids. Furthermore, when the frequency of and nature of their visits is compared to that of other insect visitors the impression is gained that masarids may prove to be of importance in the pollination of these flowers.

Collecting data and observations indicate that amongst those species which do not visit Mesembryanthemaceae, Compositae or Campanulaceae there are species which are probably of paramount importance to the plants which they patronize. Indications are that amongst these relationships there is a considerable degree of mutualism. Most notable are the relationships between *Aptosimum* and *Peliostomum* (both Scrophulariaceae) and some *Celonites* spp. *A. spinescens, A. lineare, A. depressum* and *Peliostomum virgatum* appear to be most commonly, indeed almost exclusively, to be visited by *Celonites* spp. Furthermore it has been demonstrated that *Celonites* obtaining nectar from these flowers are ideally suited to trigger the dehiscence of the anthers and to transfer pollen from one flower to another.

Also of particular interest are the relationships between *Aspalathus* (Leguminosae: Papilionatae) and *Ceramius clypeatus* and *Masarina familiaris*. Although *Aspalathus spinescens lepida* is visited by other insects including honey bees *C. clypeatus* and *M. familiaris* appear, in the Clanwilliam district at least, to be the commonest and most dependable visitors. Honey bees, for example, are not restricted to *Aspalathus* and therefore, if there is in the vicinity some plant in flower which is equally attractive or more attractive to them, they will not necessarily visit the *Aspalathus* flowers. Furthermore honey bees, when visiting the *Aspalathus* flowers, do not adopt a set stance such as do *C. clypeatus* and *M. familiaris*. It has been demonstrated that *C. clypeatus* and *M. familiaris* obtaining nectar from *Aspalathus* flowers are ideally suited to trigger the dehiscence of the anthers and to transfer pollen from one flower to another.

The present account is in its nature a preliminary review of flower visiting by masarid wasps in southern Africa. It is the authors' intention, however, to investigate further the role that masarid wasps play in the pollination of the flowers which they visit.

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Morphometrics, moult and taxonomy of the *Nectarinia afra/Nectarinia chalybea* complex of South African double-collared sunbirds

by

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ABSTRACT

Five morphological characters were measured on museum specimens of two closely related double-collared sunbird species, *Nectarinia afra* (Linnaeus) and *Nectarinia chalybea* (Linnaeus), and their wing moult was examined. The mensural data were analysed and compared statistically, to assess the validity of the races currently recognised for each species. We conclude that the races *N. c. albilateralis* Winterbottom and *N. c. capricornensis* (Roberts) are not separable, and that the races *N. c. chalybea* (L.), *N. c. subalaris* (Reichenow), *N. a. afra* (L.) and *N. a. saliens* Clancey are based on rather arbitrary grounds. Moult data support the recognition of two races in the case of *N. chalybea*, but not for *N. afra*. Clinal variation in size occurs in both species, but it is not the same in each species, nor the same for all characters. Further field study of habitat preferences, seasonal movements, and possible physiological differences is needed.

INTRODUCTION

The Greater Double-collared Sunbird *Nectarinia afra* (Linnaeus) and the Lesser Double-collared Sunbird *N. chalybea* (Linnaeus) are widely sympatric in South Africa. Both species occur in a variety of habitats from the Southwestern Cape to the Northern Transvaal (Maclean, 1985).

Currently two races of *N. afra* and four races of *N. chalybea* are recognised on the basis of distribution and morphological characters (Clancey, 1980). These races are:

Nectarinia afra afra (Linnaeus) (W. Cape to E. Cape)
N. a. saliens Clancey (Transkei to Transvaal)
Nectarinia chalybea chalybea (Linnaeus) (S. and S.W. Cape)
N. c. albilateralis Winterbottom (W. Cape coast and Karoo)
N. c. subalaris (Reichenow) (E. Cape to Natal)
N. c. capricornensis (Roberts) (Transvaal)

Mayr (1969) defines a subspecies (synonym of race) as 'an aggregate of phenotypically similar populations of a species, inhabiting a geographical subdivision of the range of a species, and differing taxonomically from other populations of the species'. This definition implies that subspecies should be allopatrically distributed, and distinguishable from each other on the basis of one or more characters. A potential problem for the subspecies concept is the variable criteria used by different taxonomists to justify subspecific separation of slightly differentiated local populations (Mayr, 1969). More recently, Mayr (p. 595 in Wiens, 1982) stated that 'the primary use of subspecies is as a sorting device in collections'. Other contributors to this discussion felt that subspecies are still useful in the study of geographical variation in birds, but much more critical assessment was required before subspecies were named. The validity of these races was assessed with such considerations in mind.

METHODS

In total 359 specimens of *N. chalybea* and 295 specimens of *N. afra* were examined. Measurements (in mm) of wing (maximum cord), bill, tarsus, tail and red breast-band width were taken using a wing rule and vernier calipers. Damaged parts of specimens were not measured. The data obtained were analysed using the following elements of the BMDP statistical package: basic data analysis (programme BMDP 1D), means cluster analysis (programme BMDP KM), and comparison of two groups with t-tests (programme BMDP 3D). First, sexual dimorphism was described for each species separately, and the sexes of each species were then compared using BMDP 1D. Secondly, male birds were grouped into "races" according to the geographical distributional limits set out in Clancey (1980), and these populations analysed and compared using BMDP 1D and 3D. Thirdly, all male specimens were

TABLE 1.

Summary of the measurements of *Nectarinia afra* and *Nectarinia chalybea*.

		Nectarinia afra				*Nectarinia chalybea*			
CHARACTER	SEX	NO. BIRDS	MEAN	SD	RANGE	NO. BIRDS	MEAN	SD	RANGE
Bill	Male	203	29,7	1,4	19,6–33,0	248	23,1	1,6	19,5–28,0
	Female	71	27,0	1,2	23,6–29,5	77	20,9	1,4	16,2–23,3
Breast-band	Male	200	20,9	2,5	14,0–29,5	208	10,6	2,6	6,0–19,0
Tarsus	Male	213	16,6	0,8	14,0–19,5	261	15,2	0,7	14,0–17,5
	Female	78	15,6	0,6	14,0–17,0	88	14,5	0,7	12,5–16,2
Wing	Male	216	65,3	2,2	59,0–71,5	270	55,3	1,8	48,5–60,0
	Female	79	59,3	1,9	54,3–65,5	89	50,5	2,1	45,5–58,0
Tail	Male	212	55,2	3,1	48,5–65,0	265	47,6	3,1	39,5–57,5
	Female	76	47,5	2,6	42,0–55,5	88	40,2	3,4	27,0–49,5

assigned to clusters on the basis of their measurements, using BMDP KM. The number of clusters was specified (two for *N. afra*, four for *N. chalybea*), but not the mid-point of any cluster. Finally the males were grouped into arbitrary allopatric geographical entities, and the character means of the group members calculated.

Moult of the primary remiges was recorded for each specimen for which date and locality information was available, using the 0–5 scoring system of Newton (1966). For males, the extent of breeding plumage and body moult was also noted. The moult sample includes 35 *N. afra* and 14 *N. chalybea* caught while bird-ringing in the Eastern Cape.

RESULTS

The male is larger than the female in all respects in both species (Table 1). There is a wide range in breast-band width in the males of both species. There is, however, little overlap in breast-band widths between the two species. The breast-band of *N. afra* is roughly twice as wide as the breast-band of *N. chalybea*, and the mean values of all measurements differ between species in both sexes, although there is some overlap.

Tables 2 and 3 compare the measurements of the races, according to the geographical divisions of Clancey (1980). Since females constituted a small part of the sample in both species, statistical comparisons are restricted to males.

Table 2.

Comparative measurements of the races of *Nectarinia chalybea*.

CHARACTER	RACE	SEX	NO. BIRDS	MEAN	SD	RANGE
Bill	*chaly*	male	43	22,3	1,3	20,5–27,0
		female	6	20,2	1,3	19,0–22,0
	albil	male	72	22,3	1,1	19,5–25,1
		female	23	19,8	1,4	16,2–23,0
	subal	male	83	24,1	1,5	20,4–27,0
		female	41	21,5	1,0	19,0–23,3
	capri	male	22	24,2	1,0	22,5–26,0
		female	4	21,0	0,9	20,0–22,0
Breast-band	*chaly*	male	37	8,7	1,7	6,0–12,0
	albil	male	52	9,1	1,8	6,2–13,7
	subal	male	74	11,7	2,2	7,5–16,0
	capri	male	27	13,6	2,0	10,0–19,0
Tarsus	*chaly*	male	43	15,1	0,5	14,0–16,0
		female	6	14,4	0,7	13,3–15,5
	albil	male	74	15,1	0,7	14,0–17,5
		female	24	14,4	0,9	12,5–16,2
	subal	male	89	15,3	0,7	14,0–16,5
		female	42	14,5	0,5	13,5–16,0

CHARACTER	RACE	SEX	NO. BIRDS	MEAN	SD	RANGE
Tarsus	*capri*	male	28	15,4	0,8	14,0–17,0
		female	13	14,6	0,7	13,7–16,0
Wing	*chaly*	male	45	54,7	1,8	48,5–57,0
		female	6	49,2	2,2	45,5–52,0
	albil	male	75	55,1	1,6	50,5–59,0
		female	24	50,0	1,9	46,0–55,0
	subal	male	91	55,7	1,8	50,0–59,0
		female	43	50,8	1,9	46,0–58,0
	capri	male	28	55,1	1,7	52,0–59,0
		female	13	51,0	2,4	47,0–56,0
Tail	*chaly*	male	45	47,3	2,4	43,5–52,0
		female	6	41,5	3,4	39,5–48,0
	albil	male	75	46,8	2,9	39,5–52,4
		female	24	39,8	3,6	32,5–49,5
	subal	male	88	48,3	3,3	41,0–57,5
		female	42	39,9	3,5	27,0–48,9
	capri	male	28	48,4	2,8	42,0–54,3
		female	13	40,4	3,1	35,5–46,5

TABLE 3.

Comparative measurements of the races of *Nectarinia afra*.

CHARACTER	RACE	SEX	NO. BIRDS	MEAN	SD	RANGE
Bill	*afra*	male	152	29,8	1,4	19,6–33,0
		female	58	27,2	1,1	24,5–29,5
	saliens	male	42	29,2	1,1	26,5–32,2
		female	10	26,2	1,4	23,6–28,0
Breast-band	*afra*	male	142	21,2	2,5	15,5–29,5
	saliens	male	50	20,2	2,4	14,0–26,0
Tarsus	*afra*	male	155	16,6	0,7	14,0–19,5
		female	60	15,6	0,6	14,0–17,0
	saliens	male	49	16,7	0,8	14,5–18,2
		female	13	15,5	0,7	14,5–16,5
Wing	*afra*	male	156	64,9	2,0	60,0–71,5
		female	61	58,8	1,7	54,3–62,5
	saliens	male	51	66,4	2,4	59,0–70,0
		female	15	60,9	2,0	58,0–65,5

CHARACTER	RACE	SEX	NO. BIRDS	MEAN	SD	RANGE
Tail	*afra*	male	153	54,6	2,7	48,5–63,0
		female	58	47,2	2,5	42,5–55,5
	saliens	male	50	56,9	3,6	49,5–65,0
		female	15	48,4	3,0	42,0–55,0

In *N. chalybea* the races *chalybea* and *albilateralis* are remarkably similar in all character means, especially with respect to bill length and breast-band width. These two races have a markedly smaller bill and breast-band than do the races *subalaris* and *capricornensis*. Tarsus length appears to vary little in different populations. No real trends between races are evident for wing and tail means.

For *N. afra* the race *afra* has a broader breast-band, while the race *saliens* has longer wings and tail. The two are similar in respect of bill and tarsus length.

If these races are compared using grouped characters, *N. c. chalybea* and *N. c. albilateralis* are the only races of *N. chalybea* that are not significantly different from each other. The two races of *N. afra* are significantly different from each other overall.

From Table 4 it can be seen that tail length is a very conservative character in *N. chalybea*, with one significant difference between any of the races compared. *N. c. chalybea* and *albilateralis* have no characters which differ significantly, while *subalaris* and *capricornensis* are strikingly different only in respect of breast-band width; *subalaris* is significantly different from both *chalybea* and *albilateralis* in most characters.

Table 4.

Statistical comparison of males of the races of *Nectarinia chalybea* on the basis of single characters.

RACE	CHARACTER	*chaly*	*albil*	*subal*
	Bill	NS		
	Breast-band	NS		
albil	Tarsus	NS		
	Wing	NS		
	Tail	NS		
	Bill	<0,001	<0,001	
	Breast-band	<0,001	<0,001	
subal	Tarsus	NS	<0,05	
	Wing	<0,05	<0,05	
	Tail	NS	<0,01	
	Bill	<0,001	<0,001	NS
	Breast-band	<0,001	<0,001	<0,001
capri	Tarsus	<0,05	<0,05	NS
	Wing	NS	NS	<0,05
	Tail	NS	NS	NS

For *N. afra*, Table 5 shows that the two races differ with regard to breast-band width, wing and tail length. Again tarsus length does not vary significantly between different populations.

TABLE 5.
Statistical comparison of males of the races of *Nectarinia afra* on the basis of single characters.

RACE	CHARACTER	*saliens*
afra	Bill	NS
	Breast-band	<0,01
	Tarsus	NS
	Wing	<0,001
	Tail	<0,001

Regional variation

There is a clear increase in bill, wing, tarsus and tail length and breast-band width of *N. chalybea* from the Southwestern Cape to the Transvaal, with a discontinuity in Natal-Transkei, where the largest mean values are found (Table 6). Except for breast-band width,

TABLE 6.
Character means of male *Nectarinia chalybea* according to region. (Sample size indicated in brackets).

REGION	BILL	BREAST-BAND	TARSUS	WING	TAIL
W. Cape (40)	21,8	7,9 (27)	15,1	54,7	46,3
S. Cape (24)	22,6	8,7 (15)	15,2	55,3	47,7
PE area (31)	22,8	10,4 (26)	15,1	55,3	47,3
E. Cape (52)	23,6	11,4 (38)	15,1	55,2	47,3
Transkei (23)	24,5	12,1 (20)	15,4	56,2	49,7
Natal (10)	25,3	12,1 (10)	15,9	56,6	49,8
Transvaal (28)	24,2	13,6 (27)	15,4	55,1	48,4

there is a very slight increase in character means between the Southern and Eastern Cape, with a much larger increase between the Eastern Cape and Natal-Transkei areas, and then a smaller decrease in character means between the Natal- Transkei and Transvaal areas.

There is an increase in tail length from the Cape through to the Transvaal in *N. afra* (Table 7). However, Transvaal birds are smaller than those from Natal and the Transkei in respect of breast-band width and tarsus length, while bill length is greatest in the Transkei, and wing length in Natal.

TABLE 7.

Character means of male *Nectarinia afra* according to region. (Sample size indicated in brackets).

REGION	BILL	BREAST-BAND	TARSUS	WING	TAIL
S. Cape (24)	28,5	20,4 (22)	15,7	63,7	54,8
PE area (28)	29,8	20,3 (25)	16,3	64,2	54,4
E. Cape (99)	29,8	21,5 (90)	16,7	65,3	54,4
Transkei (10)	30,2	20,6 (10)	16,9	65,7	55,4
Natal (13)	29,0	20,7 (12)	17,0	68,0	57,1
Transvaal (23)	29,0	19,7 (23)	16,5	66,1	58,2

Cluster analysis

For *N. chalybea*, members of clusters 3 and 4 (Table 8) have similar mean bill lengths and breast-band widths, which are distinctly smaller than those of clusters 1 and 2. There is no observable trend in the mean lengths of tarsus, wing and tail. In the case of *N. afra*, birds assigned to cluster 1 have on average longer wings and tails, but there is little difference in the means for bill and tarsus length, or breast-band width.

The distribution of cluster members for *N. chalybea* is shown in Fig. 1. Clearly, the members of clusters 1 and 2 form a distinct group in the Transvaal and Natal, whilst the members of clusters 3 and 4 form a distinct group in the Western and Southern Cape. The two clusters within each of these groups cannot be separated geographically, since the members show an almost random distribution within their region. In the Eastern Cape and Transkei the two groups of clusters intergrade. There are also singletons within the Cape which are assigned to northern clusters.

TABLE 8.

Mean measurements of the groups formed by the cluster analysis.

CLUSTER		BILL	BREAST-BAND	TARSUS	WING	TAIL
N. chalybea	1	24,8	13,8	15,4	56,9	50,8
	2	23,6	12,1	15,2	54,6	47,3
	3	22,4	8,6	15,0	55,8	50,1
	4	22,4	8,8	15,2	54,6	44,5
N. afra	1	29,4	21,1	16,8	66,7	58,4
	2	29,8	20,8	16,5	64,5	53,3

There is a large degree of overlap in the distribution of cluster members of *N. afra* (Fig. 2). There is, however, a general tendency for birds assigned to cluster 1 to be more numerous in the Transvaal and Natal, whilst the opposite is true for the Transkei and Cape where members of cluster 2 are more abundant.

The timing of primary moult

The moult data for *N. chalybea* are shown in Table 9. The records are not evenly distributed over the year, and the bulk of the material is from the Southwestern or Eastern Cape. It appears that birds from the Southern and Western Cape start the moult earlier than birds from the Eastern Cape, and Natal and Transvaal birds appear to follow the same schedule as those from the Eastern Cape. Skead (1967) indicated that breeding was more seasonal in the Western Cape than in the Eastern Cape, and this is supported by unpublished data gathered for the Atlas schemes in these areas. In the Western Cape breeding ends in October, whereas in other regions there are records for early summer as well as winter, and breeding at all seasons is possible.

For *N. afra* the majority of records are again from the Eastern Cape (Table 10). In this case there is no indication of regional differences in the timing of moult, nor is there a clearly defined breeding season for any part of the bird's range (Skead, 1967; Tarboton *et al.*, 1987; unpubl. data).

In both species, males in full breeding plumage have been recorded throughout the year. Birds in partial breeding plumage may be sub-adult males, acquiring adult plumage for the first time. The months in which such specimens have been collected are in accordance with the known breeding times for the areas concerned. Males and females moult at the same time of the year.

DISCUSSION

The two species differ significantly with respect to most single characters, and are certainly separable on the basis of pooled characters. Tarsus length seems to be least variable in both species. There is little or no overlap in bill lengths of both species, and although there is wide intraspecific variability in breast-band width, there is little interspecific overlap, with *N. afra* having a red band approximately twice as wide as that of *N. chalybea*. The commonly-used

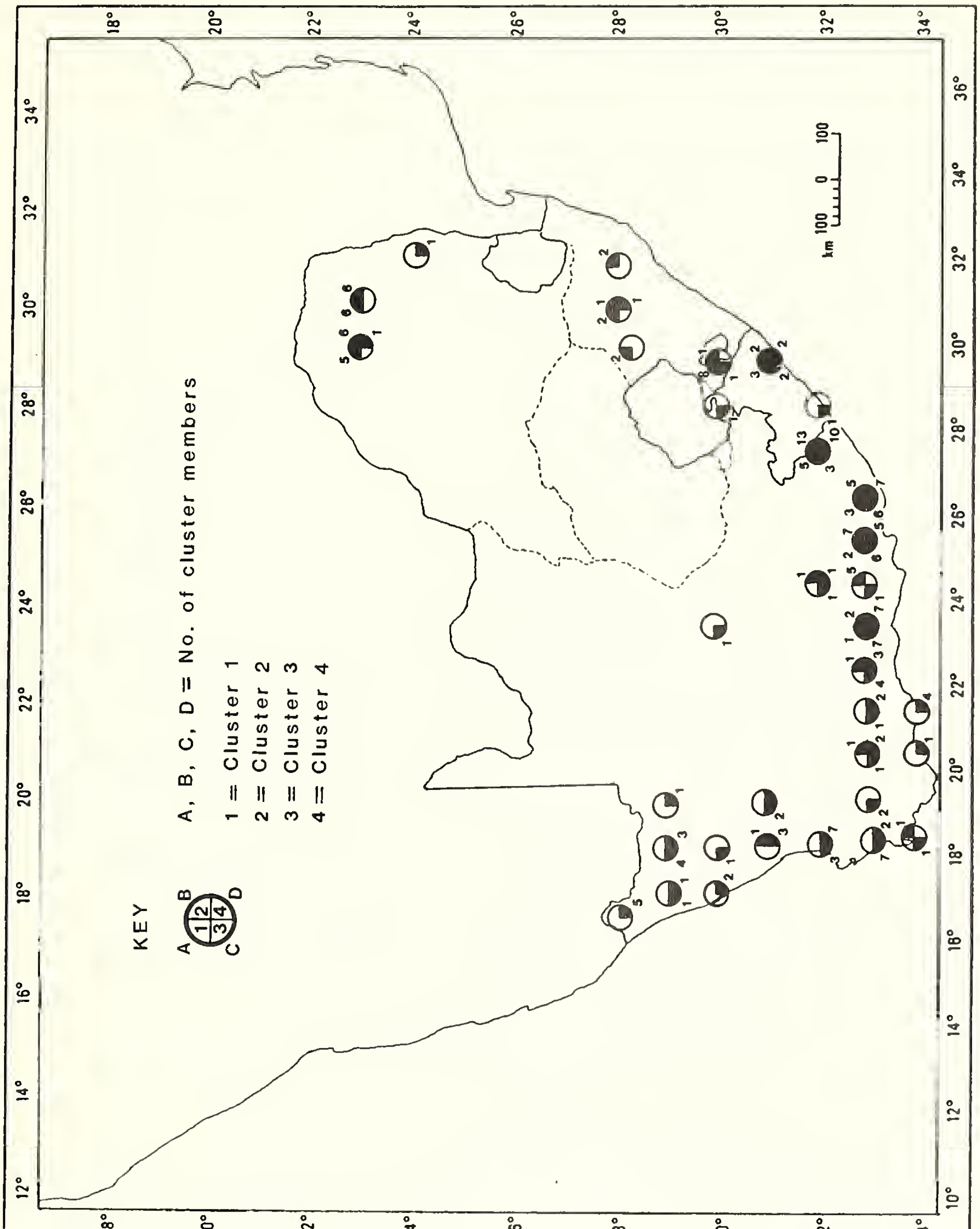

Fig. 1. Map of South Africa showing the geographical distribution of *Nectarinia chalybea* members of the computer-generated clusters based on morphological similarity.

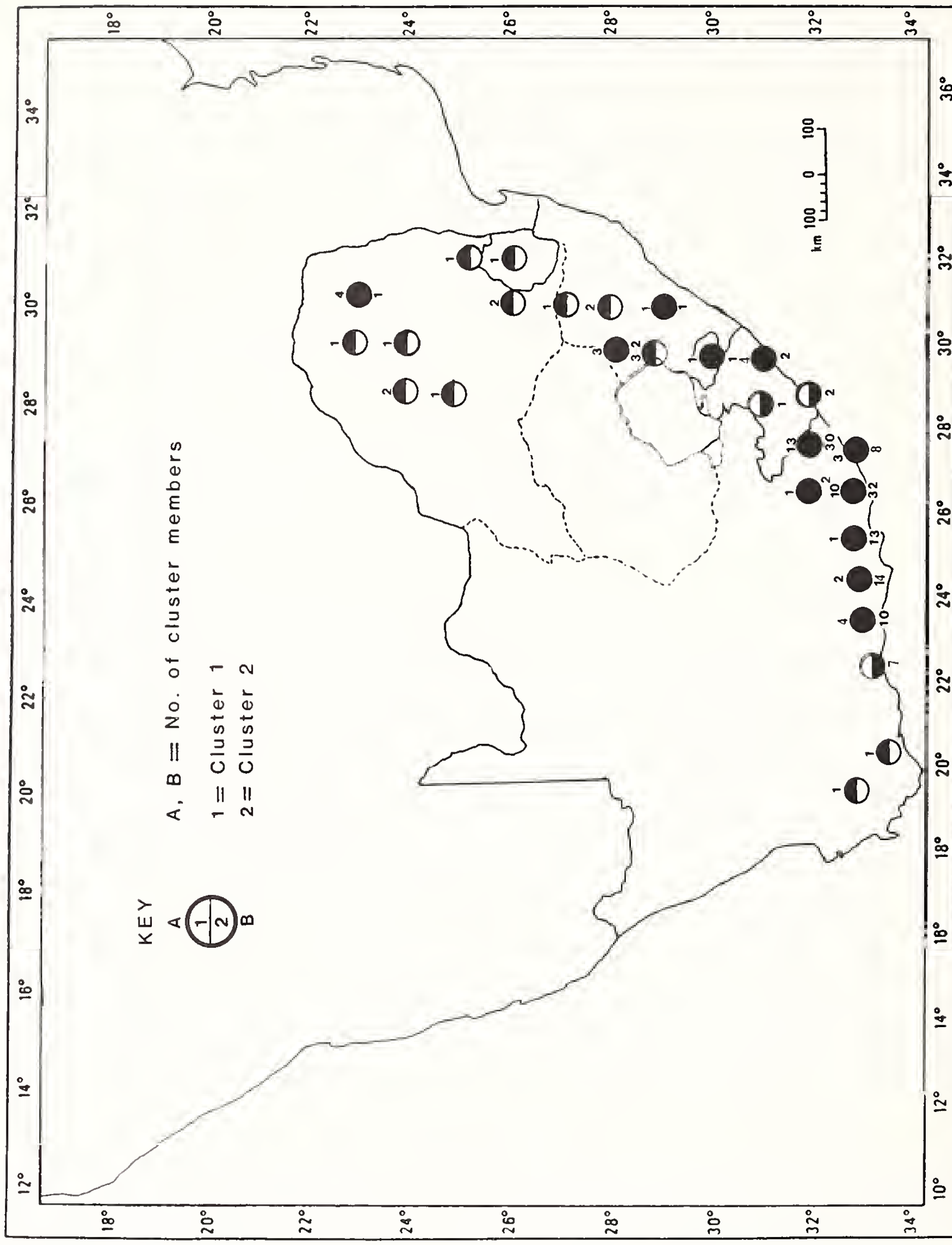

Fig. 2. Map of South Africa showing the geographical distribution of *Nectarinia afra* members of the computer-generated clusters based on morphological similarity.

TABLE 9.

The timing of primary moult in *Nectarinia chalybea*.

MONTH	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
NO. BIRDS (E. CAPE)	7	12	13	14	17	6	14	12	23	11	2	9	140
% OF TOTAL IN MOULT	11	27	32	13	0	0	0	0	0	0	4	13	37
NO. BIRDS (S.W. CAPE)	0	1	12	9	4	0	5	13	5	16	9	1	75
% OF TOTAL IN MOULT	0	0	0	0	0	0	0	0	0	56	38	6	16
NO. BIRDS (TVL, NTL, TRANSKEI)	14	0	2	4	1	2	3	5	3	2	5	7	43
% OF TOTAL IN MOULT	59	0	17	8	0	0	0	0	0	0	8	8	12

TABLE 10.

The timing of primary moult in *Nectarinia afra*.

MONTH	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
NO. BIRDS (CAPE PROV.)	27	22	11	15	25	13	25	8	29	19	11	4	209
% OF TOTAL IN MOULT	35	33	13	2	0	6	1	0	2	2	2	4	53
NO. BIRDS (TVL, NTL, TRANSKEI)	2	0	1	3	4	3	2	2	4	0	3	4	28
% OF TOTAL IN MOULT	40	0	20	20	0	0	0	0	0	0	0	20	5

identification guide of a twofold difference in bill size and red breast-band for these two species (Skead, 1967), therefore applies in the general sense.

The races of Nectarinia chalybea

Winterbottom (1963) distinguished the race *N. c. albilateralis* solely on the basis of a whiter flank coloration in the males. However, Clancey and Irwin (1978) state that this colour difference is due to salt-bleaching and wind borne sand abrasion affecting the birds breeding on the white sand dunes of the Western Cape. If this is the case, why did Winterbottom not note such colour differences in the females as well? Clancey and Irwin (1978) justify the recognition of the race on 'the plain rump in males and the lack of a yellowish tinge to the lower ventral surface in freshly moulted males'. The relevance of plumage differences in these regions for the

birds themselves is questionable; it seems likely that breast-band and song characters are the key features in both male-male and male-female interactions. Winterbottom (1963), in the original description of *N. c. albilateralis*, makes no mention of these colour differences. He concludes that the female *N. c. albilateralis* is not distinguishable from *N. c. chalybea*, whereas Clancey and Irwin (1978) state that the female is paler and less olive above (Light Brownish Olive versus Buffy Olive in *N. c. chalybea*), and 'distinctly less greenish yellow' below, being 'pale greyish olive buff'. The publications of Winterbottom (1963) and Clancey and Irwin (1978) are the only papers dealing with the taxonomy of *N. c. chalybea*, and it would seem that confusion about the true colour differences exists. We badly need a system of colour measurement which allows for independent assessment and comparison of colour differences.

Winterbottom (1963) cites the measurements of 19 male *N. c. albilateralis* and Clancey and Irwin (1978) 12 males. None of these measurements is significantly different from those of *N. c. chalybea*, and in this study a statistical comparison of the two races also found no significant differences in any of the characters measured (Table 4).

Clancey and Irwin (1978) also cite a wider breast-band as a difference (7–8 mm for *albilateralis* versus 10 mm for *chalybea*). The data from Table 2 certainly do not support this, since here *albilateralis* has a slightly wider breast-band on average. It would seem therefore that there is no quantitative morphological basis for the separation of *chalybea* and *albilateralis*. This conclusion is further supported by the regional comparisons in Table 6, which indicate the occurrence of a cline, defined by Mayr (1969) as a character gradient. Winterbottom (1963) found a simple cline from north to south in culmen length for the species as a whole, whilst the variation in wing length was from a maximum in the central part of the range (Natal and Transkei) to minima north and south. Exactly the same trends are found in this study (Table 6). From Winterbottom's results, it can be seen that the distributions of both *N. c. albilateralis* and *N. c. chalybea* lie along this cline. There will therefore be no independent variation in character measurements, thus reducing the likelihood of individuals of both subspecies being different at the same point along the cline. The implications of clinal variation for the taxonomy of a species is discussed later. Clancey and Irwin (1978) divided *chalybea* and *albilateralis* distributionally on the basis of habitat, with *albilateralis* occupying the arid karroid scrub region, and *chalybea* the wetter mountains and coastal region of the Southern and Southwestern Cape. Our data suggest that this division is artificial in morphological terms. This implies that the two subspecies proposed by Clancey (1978) are not allopatrically distributed, which, according to Mayr (1969) strongly indicates a wrong usage of the term 'subspecies'. This is discussed more fully later. The validity of the subspecies *N. c. albilateralis* is therefore highly questionable.

Clancey (1975) decided to resurrect *N. c. capricornensis* (Roberts) as a minor subspecies on the basis of its smaller size. Previously, *capricornensis* was treated as synonymous with *subalaris*. The main subspecific difference from *N. c. subalaris* (Reichenow) is a shorter wing (Clancey and Irwin, 1978). They give measurements of 12 males and three females of *subalaris* and 11 males and nine females of *capricornensis*. In this small and select sample, wing lengths show almost no overlap between subspecies for both sexes; male culmen lengths are similar, but with those of *subalaris* tending to be slightly larger; female culmen lengths show virtually no overlap; male tail lengths show a fairly large overlap, but *subalaris* has a longer tail on average; and female tail lengths are very similar, but with *subalaris* again slightly longer. It is probably correct to say that *subalaris* is larger than *capricornensis*, but in the light of this study using a much larger sample size, the significance of the size differences is questionable (Table 2). Male *subalaris* have slightly

larger tarsus, wing and tail means than male *capricornensis*, but the comparative analyses using t-tests show no significant difference in tarsus and tail lengths (Table 4). Wing lengths are marginally significantly different. There is certainly a far greater overlap in measurements than is suggested by Clancey and Irwin's (1978) data. A pooled comparative analysis does find a significant difference between the two races, but this result depends primarily on the wider breast-band of *capricornensis*. The data on the females (Table 2) come from a smaller sample, and indicate a similarity in all measurements with no trends in size differences evident.

Clancey and Irwin (1978) state that *N. c. subalaris* differs taxonomically from the nominate race *N. c. chalybea* in being larger, with a longer bill. The data obtained from this study support these size differences. In both males and females (Table 2), *subalaris* has a larger mean for all characters (except female tail length). The comparative analysis of males (Table 4) shows, however, that tarsus and wing length are not significantly different statistically.

The results of Table 6, which are supported by a similar study by Winterbottom (1963), are strong evidence for the existence of a cline in size variation of *N. chalybea*. This brings the validity of subspecies in *N. chalybea* as a whole into question. It can be seen from the table that there is a regular cline in breast-band measurements, with an increase in mean size from the Southern Cape through to the Transvaal. A similar pattern is observed for bill, tarsus, wing and tail measurements but with the largest means occurring in Natal. Mayr (1969) states that 'when the geographic variation of a species is clinal, it is usually inadvisable to recognise subspecies, except possibly for the two opposite ends of the cline when they are very different or separated by a pronounced step'. If one calculates the differences between the means for adjacent geographical regions in Table 6, there is a pronounced step in the differences for all characters except breast-band width between the Natal-Transkei and Eastern Cape groups. At this point, the geographical plot of the four clusters generated by the computer (Fig. 1) proves useful. Clusters 1 and 2 form a distinct group in the Transvaal and Natal-Transkei, whilst clusters 3 and 4 form a distinct group in the Southern and Western Cape. The two groups of clusters intergrade in the Transkei and Eastern Cape regions. It is quite possible that, should the breast-band measurements be removed from the cluster analysis, a sharper distinction between the two groups may be found in the intergrade regions. Table 6 shows breast-band width to be very similar in these two areas but quite different in the adjacent Southern Cape and Transvaal areas.

The moult data also suggest that *N. chalybea* can be divided into two populations with respect to the timing of wing-moult. Birds from the Southern and Western Cape start the moult as early as October, while those from the Eastern Cape start moulting in December (Table 9). However, the boundary between the two "moult regions" is not clearly defined on the basis of the present data. Birds from Knysna (34°02′S, 23°03′E) may belong to the Eastern Cape, on the strength of a specimen from Knysna which is moulting in April, much later than is typical for Southern Cape birds from areas such as Mossel Bay. It appears that the division on the basis of moult will lie well to the east of the morphological boundary between the groups defined above. It is of course not certain that moulting seasons are genetically determined rather than responsive to environmental conditions, and although this may be the case in some species (*cf.* Craig, 1988) it should not be assumed to constitute a general rule. The Eastern Cape does form a transitional zone in many respects, and this may explain why a change in moult timing occurs at this point rather than further east in a climatically more predictable zone.

It has been argued above that *albilateralis* is not morphologically separable from *chalybea*, and that *capricornensis* is not separable from *subalaris*. However, in mensural characters, both

subalaris and *capricornensis* are significantly different from both *chalybea* and *albilateralis* (Table 4). Furthermore, the division in the distribution between *subalaris* and *albilateralis* occurs in the Eastern Cape, where a pronounced step in the clines of bill, tarsus, wing and tail length occurs. The moult data also divide the species into two groups. We propose that the number of subspecies be reduced from four to two, through the fusion of *albilateralis* with *chalybea* and the fusion of *capricornensis* with *subalaris*. Indeed, prior to 1963, only two subspecies of *N. chalybea* were recognized, namely *N. c. chalybea* and *N. c. subalaris* (Clancey, 1962).

*The races of **Nectarinia afra***

Clancey (1962), in his description of *N. a. saliens* as a new subspecies of *N. afra*, cited both colour and size differences to support his decision. He stated that the male *saliens* differs from *afra* 'in having the non-metallic lower ventral surface lighter and more yellowish in freshly moulted dress, less dark and brownish (Ecru Olive as against Citrine Drab)'. The female *saliens* is described as 'less dark and greyish and markedly reticulate over the throat and breast, and more saliently greenish or yellowish over the medial lower ventral surface less grey (about Barium Yellow abdominally)'. Clancey (1962) also stated that *saliens* is larger than *afra*. From a sample of 14 *saliens* and 63 *afra* he presented measurements that are not only highly significantly different, but also show no overlap whatsoever between the two subspecies. Taken at face value, such measurements would strongly support the division of *N. afra* into two subspecies. On the other hand, the results of this study, using a larger sample size, show a very wide overlap in character measurements (Table 3). Most of the specimens studied, however, came from the Eastern Cape area (Fig. 2), a region where Clancey (1962) claimed that the two subspecies intergrade. Table 7 suggests a possible cline in different character measurements, with bill length and breast-band width decreasing from the Cape to the Transvaal, tarsus length being very constant, and wing and tail length increasing from the Cape to the Transvaal. The clines for wing and tail length, and bill and breast-band, thus occur in opposite directions. As already mentioned, Mayr (1969) states that it is inadvisable to divide a species into subspecies along a cline, except possibly for the two opposite ends of the cline when they are different or separated by a pronounced step. Clancey's (1962) samples are definitely very different between the two subspecies. The comparative analysis of males in this study also finds a significant difference between the two races (Table 5). There may, therefore, be grounds for the subdivision of *N. afra* into two subspecies. On the other hand, the clines appear to be rather smooth, with no pronounced step (Table 7) at the area proposed by Clancey (1962, 1980) as the boundary between the two subspecies, namely the Transkei-Eastern Cape border. Again, the distributional plot of two clusters generated by the computer (Fig. 2) may prove useful. This shows a very wide overlap in the distribution of clusters 1 and 2, and serves as further evidence to suggest the clines in the characters of *N. afra* are very smooth. Moult data (Table 10) do not suggest any regional variation in the timing of wing-moult, although the samples for Natal and the Transvaal are small. Further study is required to resolve the problem, but we would question whether the recognition of subspecies in *N. afra* is justified.

So far, the 'significant differences' between the populations of birds discussed have been based on the grouping of individuals from allopatric areas, and then comparing the averages obtained for each group. This study has shown the occurrence of great variation within each of these groups, and the existence of clines in character measurements. The borders of the areas used in the analysis of clines were arbitrary. The delimitation of the distributional range and the description of each subspecies seems to have involved a critical sample size never greater than

20 (Clancey, 1962, 1975; Clancey and Irwin, 1978; Winterbottom, 1963). The probability of such small, and often obviously select samples being adequate to describe geographical variation is slight. The subspecies currently recognised for *N. afra* and *N. chalybea* thus appear to be poorly defined units. After all, if a cline exists through the distribution of a species, it can be split up into a variable number of populations using any boundaries, which are subsequently found to separate 'significantly different' groups.

N. chalybea shows a wide tolerance of habitat, being found from the dry karroid scrub of the Southwestern Cape to wet forests in northern areas of its range. Despite this wide tolerance, Skead (1967) reports that where the *N. chalybea* overlaps with *N. afra* in the dry Valley Bushveld and Macchia of the Southern and Eastern Cape, the former inhabits forest and seldom ventures into the more open thornveld which is the favoured habitat of *N. afra*. The latter is reported to avoid forests, only venturing into forest edges and narrow strips of dune forest that are bushier and less well-treed. Tarboton *et al.* (1987) report that, in the Transvaal, *N. chalybea* is found in montane forest and its edges, whilst *N. afra* occurs in more open, hilly country, especially where aloes are concentrated. These differences in habitat preference are also supported by Maclean (1985), and Hall and Moreau (1970). In the Western Cape, where *N. afra* and the Black Sunbird *N. amethystina* do not occur, *N. chalybea* prefers the macchia scrub to the forest (Skead, 1967). During the course of field observations in the Eastern Cape the two species were only observed together in forest-edge situations and in suburban gardens. The latter is an artificial habitat, and with large numbers of cultivated flowers, nectar will usually be more abundant than in the adjacent natural habitats.

It is possible that *N. chalybea*, owing to its smaller size, has been out-competed in the habitats occupied by its larger relatives, especially the very closely related *N. afra*, and become adapted to a different ecological habitat. Since the African sunbirds commonly puncture the base of flowers to obtain nectar which they cannot otherwise reach (Skead, 1967; pers. obs.), differences in bill size are unlikely to be associated with different flower preferences. However, the importance of insect food to sunbirds, and the role of bill morphology in prey capture, need further study. Variations in bill size follow a similar geographical trend in both these species (see Tables 6 and 7), and the present data provide no suggestion that morphological changes can be ascribed to interspecific interactions in sympatry.

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Notes on nesting behaviour in *Bembix bubalus* Handlirsch in southern Africa with the emphasis on nest sharing and reaction to nest parasites (Hymenoptera: Sphecidae)

by

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(Albany Museum, Grahamstown)

ABSTRACT

Data on the nesting behaviour of *Bembix bubalus* Handlirsch are presented. Of particular note is an instance of nest sharing as this appears to be the first record of nest sharing by a progressive provisioner in the Sphecidae. An instance is recorded of a wasp provisioning, in addition to its own larva, the larvae of a sarcophagid fly which had parasitised the nest.

INTRODUCTION

Due to the current interest both in nest sharing and in response to parasitism it seems useful to publish this account of the nesting of *Bembix bubalus* despite its preliminary nature, particularly as opportunities for such studies are not as common in southern Africa as might be supposed.

The present paper is based on a preliminary investigation of three days duration carried out during a short visit to the Oudtshoorn district in December 1986. A follow up investigation was planned for January 1987 but due to unforeseen problems a second visit to the area in the summer of 1986/1987 did not come about. The site was revisited in December 1987, that is in the following summer. Unfortunately, whereas there had been a thousand or more individuals of *Bembix bubalus* nesting there, when the preliminary observations were made, there were then fewer than a dozen wasps attempting unsuccessfully to excavate nests. The sand had become so destructured, due to drought and trampling, that their efforts were in vain. This decline in nesting activity was particularly disappointing as, in the course of their investigations of the nesting of wasps in the arid areas of southern Africa during the past two decades, the authors had not previously found any species of *Bembix* nesting in aggregations of more than about a dozen. Nesting aggregations of several hundred (Evans, 1957) or thousand (Bequaert, 1932) have, however, been reported for some species of *Bembix* elsewhere in the world.

THE NESTING OF *BEMBIX BUBALUS* HANDLIRSCH

Description of the nesting area

The nesting aggregation covered an area, approximately 300 m^2, of level friable sandy soil

Fig. 1. Nesting area of *Bembix bubalus* Handlirsch at Onverwacht, Oudtshoorn district.

sparsely vegetated. The site lies on the flood plain of the Kammanassie River at Onverwacht (33° 37′ 35″S, 22° 14′ 18″E) to the south of Oudtshoorn in the Little Karoo.

This area situated immediately inland of the Outeniqua Mountains lies in a rain shadow and consequently receives an annual rainfall of only 240 mm. Rain may fall during any season of the year, however, spring and late summer are the wettest periods. The soils above the flood plain are relatively coarse grained and are of the Cretaceous Enon Formation. Those of the flood plain on which the nesting site of *B. bubalus* is situated are light coloured, finer textured and are of diverse provenance having been carried down from further east by the river. The area lies within Acocks' Veld Type 26, False Karroid Broken Veld (Acocks, 1953, 1975 and 1988). The area is characterized by dwarf scrub, with a noticeable succulent element, and with taller shrubs mainly along the water courses (Fig. 1).

Nest excavation and temporary closure

The nests were excavated in the usual *Bembix* manner: that is the two fore-legs, equipped with sand rakes, were repeatedly swept back in unison whilst the abdomen was synchronously raised and lowered allowing the soil to be shot out behind the wasp.

The spoils of excavation were drawn back to some little distance from the nest entrance where they accumulated to form a tumulus up to 65 mm in diameter. Throughout nest excavation and provisioning the tumulus was not dispersed by the wasp.

Fig. 2. Female *Bembix bubalus* Handlirsch in flight carrying her prey, a bombyliid fly, held ventral side up close beneath her.

Nests were temporarily sealed with sand when wasps were away from them and when wasps were within them but not actively working, for example in cloudy weather or at night.

During nest excavation miltogrammine flies were observed stationed on perches, such as nearby twigs, in close proximity to nests. From their behaviour it was clear that they were monitoring the wasps' nesting activities.

Male behaviour

Males were common in the nesting area during the period of the investigation 10–12.xii.86 when nesting by a thousand or more females was in full swing. They were seen to fly rapidly low over the ground frequently changing direction and patrolling the entire area of the nesting aggregation.

At the time of the second visit to the study site on 8.xii.87 when there were fewer than a dozen females attempting to nest only one male was observed. This male was actively interested in all the females. Each time he spotted a female he advanced towards her with a markedly high pitched buzzing flight, came above her and tapped her with his abdomen. Only one female was seen to accept his advances, that is to permit him to grasp her and to fly off with her. Actual copulation was not observed.

Identity of the prey, carriage of the prey and satellite flies

Seventy eight prey were obtained, 24 from females captured flying with prey and 54 from nests (Table 1). The latter category was made up of complete prey and prey in the form of recognizable remnants. All prey were flies, the vast majority (91%) being flower-visiting flies of the families Bombyliidae and Syrphidae, suggesting that *B. bubalus* seeks prey at flowers.

Although actual prey capture was not witnessed large numbers of wasps were observed flying with prey. In many instances these wasps were accompanied by satellite flies. The prey fly is held ventral side up, close beneath the wasp by her middle-pair of legs when she is in flight (Fig. 2). On nearing her nest the wasp moves the fly back (Fig. 3) so that her approach to the nest is very "tail heavy". She alights at the concealed nest entrance and immediately clears the sand with her fore-legs whilst standing on her hind-legs (Fig. 4) and continuing to hold the prey with her middle-legs. Opening of the nest and entry into it are rapid so that little opportunity is given to the satellite flies for larviposition.

Of interest was the observation of a female which due to some disturbance dropped her prey, a large syrphid, and without hesitation returned, dived down and picked up her prey without alighting.

Description of twelve nests, the nature of their contents and a record of the presence of three wasps in a nest

A sample of twelve nests was excavated. Nine of these were unicellular and of a typical basic

Fig. 3. A female *Bembix bubalus* Handlirsch in flight carrying her prey, a syrphid fly (*Eristalinus taeniops* (Wied.)), and preparing to land.

TABLE 1.

Prey of *Bembix bubalus* Handlirsch taken with wasps in flight and from the nests excavated at Onverwacht, Oudtshoorn district, 9–12 .xii.86.

Identity of prey	no. taken with wasp in flight	no. taken from nest										no.total
		1	2	3	4	5	6	7	8	9	10	
?STRATIOMYIDAE												
?Genus and species	—	—	—	—	—	—	—	—	1	—	—	1
TABANIDAE												
Chrysops obliquifasciata Macquart	—	—	—	—	—	—	—	—	—	1	—	1
BOMBYLIIDAE												
Bombylius discoideus F.	1	—	—	—	—	—	—	—	—	—	—	1
Bombylius ornatus Wied.	2	—	—	1	—	—	—	—	—	1	—	4
Bombylius ?sp.	—	—	2	—	—	—	—	1	—	—	—	3
Exoprosopa sp. A	—	1	—	—	1	—	1	—	—	—	—	3
Exoprosopa sp. B	—	—	—	—	—	—	1	—	—	—	—	1
?*Exoprosopa*	—	1	—	—	—	4	—	—	—	1	—	6
Systoechus sp. A	5	—	1	1	1	5	2	—	—	—	—	15
Systoechus sp. B	1	—	9	—	—	—	—	—	—	—	—	10
Villa sp. A	—	—	—	—	—	—	—	—	—	—	1	1
Villa sp. B	2	—	—	—	—	—	—	—	—	—	—	2
?Genus and species A	—	1	—	—	—	—	—	—	—	—	—	1
?Genus and species B	—	—	—	—	—	1	—	—	—	—	—	1
												48
SYRPHIDAE												
Allograpta calopus Wied.	—	—	—	1	—	—	—	—	—	—	—	1
Eristalinus taeniops (Wied.)	5	8	—	—	1	1	—	—	—	—	—	15
Eristalis tenax (L.)	5	—	—	—	—	—	—	—	—	—	—	5
?Genus and species A	—	—	—	—	1	—	—	—	—	—	—	1
?Genus and species B	—	—	—	—	1	—	—	—	—	—	—	1
												23
MUSCIDAE												
Musca sp.	1	—	—	—	—	—	—	—	—	—	—	1
SARCOPHAGIDAE												
?Genus and species	—	—	—	—	—	—	1	—	—	—	—	1
TACHINIDAE												
?Genus and species A	—	1	—	—	—	—	—	—	—	—	—	1
?Genus and species B	1	—	—	—	—	—	—	—	—	—	—	1
?Genus and species C	1	—	—	—	—	—	—	—	—	—	—	1
												3

Fig. 4. A female *Bembix bubalus* Handlirsch holding her prey, a syrphid fly (*Eristalinus taeniops* (Wied.)), with her middle-legs whilst standing on her hind-legs and opening her nest with her fore-legs.

Bembix nest pattern (Evans, 1957 and Gess, 1986), that is, with a short sloping entrance burrow dipping down to end in a spur and giving rise just above the spur to a secondary shaft ending in a large ovoid cell (Fig. 5). Of the three remaining nests one was two-celled, one three-celled and the third four-celled (Fig. 6). Shaft diameter was 9–9,5 mm, cell diameter 12,5–14 mm and cell depth 130–170 mm.

Six of the unicellular nests each contained a wasp larva with one or two prey flies and fly fragments. Two were empty. The ninth contained a wasp larva, three large sarcophagid maggots, two small sarcophagid maggots, eleven partially eaten prey flies and fly remains.

Only one cell in each of the two-celled nests and in the three-celled nest contained a wasp larva and prey flies.

In the four-celled nest two of the cells contained cocoons and fly remains, the third a large wasp larva and fly remains, and the fourth a small wasp larva, fly remains and a freshly introduced prey fly. One female had been observed taking a fly into the nest and a female, presumed to be this female, had been captured when she was leaving the nest. The nest upon excavation was found to contain two additional females. Each was positioned facing outwards within a cell containing a feeding larva which she appeared to be guarding.

It is noteworthy not only that three females should have been present in the nest but that, that being so, there were only two wasp larvae being actively provisioned.

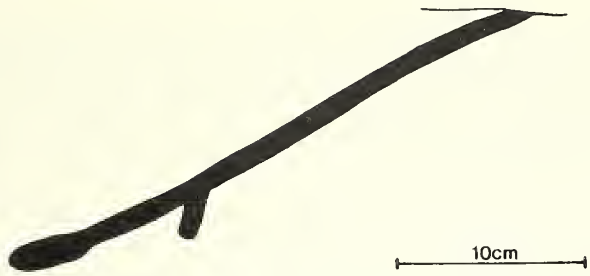

Fig. 5. Plan of a unicellular nest of *Bembix bubalus* Handlirsch investigated at Onverwacht, Outshoorn district, 10–12.xii.86

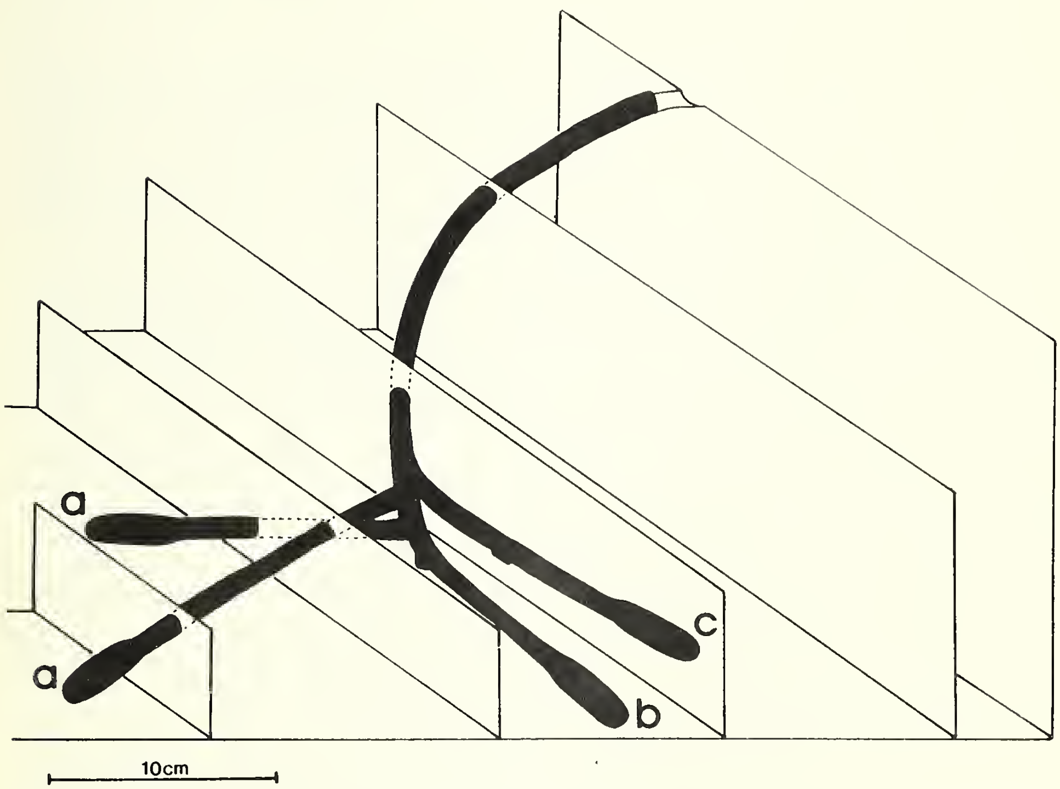

Fig. 6. Plan of the four-celled nest of *Bembix bubalus* Handlirsch investigated at Onverwacht, Oudtshoorn district, 10–12.xii.86: **a**–cell containing wasp-cocoon and fly remains; **b**–cell containing large wasp-larva and fly remains; **c**–cell containing small wasp-larva, entire fly and fly remains.

Visits to nests by more than one female

It was observed that in several instances nests were being visited by more than one female. Furthermore when two females had entered a nest neither was evicted. During the short period of the study, three days, during which provisioning of nests was being actively pursued no case of two or more females taking prey into a nest was noted. It is therefore not known whether any one nest was being provisioned by more than one female.

Provisioning mode

In common with the majority of species of *Bembix, B. bubalus* is clearly a progressive provisioner, that is the larva is provided with fresh prey throughout its development.

Voltinism

B. bubalus is clearly bi-voltine or multivoltine as an adult emerged before the end of the 86/87 summer season from a cocoon obtained from one of the cells of the four-celled nest.

DISCUSSION

It seems of interest to consider whether the findings for *B. bubalus* are of any particular significance in a consideration of the ethology of Sphecidae and of solitary aculeate wasps as a whole.

The points to be considered are: the variation in the number of cells; the presence of three wasps in one of the nests in relation to the development of presocial behaviour; and the wasp's reaction to the presence of sarcophagid maggots in her nest.

The variation in the number of cells in itself is not of particular note. Tsuneki (1956), in Japan found that, though the nest of *Bembix niponica* F. Smith is typically unicellular, in some nesting aggregations about 4% of the nests were compound and in one exceptional aggregation the majority of nests contained two or more cells. Further, observations on *Bembix nubilipennis* Cresson in North America (Evans, 1966) suggest that that species when bi-voltine may make multi-cellular nests in spring and unicellular nests in autumn.

What is, however, of note is that the four-celled nest of *B. bubalus* was occupied by three wasps. It would appear therefore that *B. bubalus* practises facultative nest sharing. The nearest recorded approach to this condition in *Bembix* seems to be the observation by Evans (1966), in North America, that in *Bembix amoena* Handlirsch nesting aggregations, where nests are in very close proximity, one nest entrance may serve more than one nest. However, in that species the burrows diverge immediately beneath the ground surface so that there is only entrance sharing, not nest sharing as exhibited by *B. bubalus*.

Observations that two wasps could enter a nest without either being evicted and that one nest was found to be occupied by three wasps is indicative of a breakdown in territoriality, which is a pre-condition to nest sharing and co-operative behaviour.

Relatively few studies of Sphecidae provide evidence of co-operative behaviour. An interesting example of differential aggression is exhibited by the mass provisioning nyssonine *Sphecius speciosus* Drury (Pfennig and Reeve, 1989) which tolerates the intrusion of large near neighbours into the nest but only when no prey cicada is exposed. Examples of actual nest sharing have been recorded for species in the sub-families Sphecinae (Brockmann and Dawkins, 1979; Brockmann, Grafen and Dawkins, 1979; Eberhard, 1972 in Evans, 1977), Pemphredon-

inae (Matthews, 1968 in Evans, 1977), Crabroninae (Bowden, 1964; and Evans, 1964 and Peters, 1973 both in Bohart and Menke, 1976) and Philanthinae (Alcock, 1975; Evans, 1973; Evans and Hook, 1982a, 1982b, and 1986; Hook, 1987). All are for mass provisioners, that is all the provision required for the development of the larva is generally provided before the hatching of the egg. The present record for *B. bubalus* is therefore probably the first for nest sharing by a nyssonine and is also probably the first example of nest-sharing by a progressive provisioner to be recorded for the Sphecidae. That *B. bubalus* is a progressive provisioner is of particular interest as it therefore exhibits a combination of para-social behaviour, that is adult females of the same generation associate in a common nest, and sub-social behaviour, that is the larvae are cared for by a parent for some time after hatching. This behaviour combination has otherwise, for wasps, been recorded only in the Vespoidea. Furthermore as *B. bubalus* is at least bi-voltine the possibility exists that wasps of two generations may come into contact in a nest.

At this point it is of interest to consider the accounts of Alcock (1975), Evans and Hook (1982a, 1982b and 1986) and Hook (1987) of nest sharing by some species of *Cerceris* (Philanthinae). Some evidence was obtained of differentiation in the roles of the females associated with the nest. Some appeared to be provisioners and others non-provisioners. Females of both types showed mandibular wear, suggesting that both were involved in preparing cells, also both types had ovaries containing well-formed oocytes, which suggested that both laid eggs more or less regularly. Non-provisioners were considered to perform an important function as guards but no suggestion was made as to what factors determine whether a female is a provisioner or not.

The fact that in the four-celled *B. bubalus* nest three females were present but only two cells were being provisioned and that both of these were being guarded leads one to ask whether there is here too some degree of division of labour or co-operation between the females.

Finally it is of interest to consider the response by *B. bubalus* to nest parasites. It has been suggested that gregarious nesting may be a "selfish herd" response to parasites and Wcislo (1984) sees parasites as important agents of selection for the maintenance of aggregations and thus for more advanced social levels as well. Evans and Hook (1986) in their study of *Cerceris* were satisfied that there is little doubt of the importance of guards in protecting the nest contents from invasion by ants and mutillids. On the other hand they found that flies which operate at the nest entrance are not deterred by guards, in fact, the delay sometimes caused by the guard to a prey-laden wasp entering the nest actually enhanced the attack by satellite flies which larviposit on the prey at the nest entrance. As *Cerceris* is a mass provisioner the introduction of fly maggots into the cell results not only in the consumption of the available prey but also of the wasp larva. *Sphex decipiens* Kohl (Sphecinae), the nesting of which was studied in the Grahamstown district by Gess and Gess (unpublished field notes, 1985/1986), which is a mass provisioner suffers a high incidence of loss of provision and larvae to the ravages of fly maggots. Evans (1966) suggested that in the case of progressive provisioners the fly maggots would most probably be detected and destroyed, and goes as far as to say that in the genus *Bembix* progressive provisioning has led to parasitism by miltogrammine flies being reduced to virtually zero (Evans, 1977).

This might well be the case in species which clean out their nests. The presence of fly remains in cells of *B. bubalus* containing cocoons indicates that this species does not clean out its cells. It was therefore of interest to discover its reaction to the presence of fly maggots in its cells. One single-celled nest was found to have been so parasitised. The cell which was still being actively provisioned contained a large wasp larva, three large fly maggots and two small fly

maggots. The wasp had not as one might have expected destroyed the fly maggots or abandoned the nest but was provisioning the maggots as well as her own larva. In doing so the wasp undoubtedly saved her larva from destruction by the maggots, however, she had succeeded in rearing only one wasp offspring when she might have reared several had she not been provisioning the maggots. Had she been a mass provisioner her energies would not have been wasted in this way. This seems a curiously disadvantageous result of what would otherwise appear to be an advanced behaviour pattern.

Clearly investigation of many more nests is required before any more definite statements can be made concerning: the incidence of nest sharing: the nature of and degree of co-operation between wasps sharing a nest: and the incidence of and response to nest parasitism.

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Early ontogeny and notes on breeding behaviour, habitat preference and conservation of the Cape kurper, *Sandelia capensis* (Pisces: Anabantidae)

by

J. A. CAMBRAY

(Albany Museum, Grahamstown, 6140, South Africa)

ABSTRACT

The development of the eggs, free embryos and larvae of *Sandelia capensis* is described from laboratory-reared specimens.

The eggs had 1,0–1,4 mm diameters, adhesive egg envelopes, narrow perivitelline spaces and single oil globules 0,62 mm in diameter. The eggs were negatively buoyant.

The free embryos hatched at a premature ontogenetic stage and were 3,0–3,6 mm NL. They attached themselves to objects using the adhesive surface on the dorsum of their heads. At 4,7 mm NL the oil globule began to migrate dorsally and divided into a right and a left globule and during that period the swimbladder inflated. These asymmetrical oil globules disappeared at between 6,3–6,9 mm NL. The swimbladder began to extend posteriorly at 6,25 mm SL and reached maximum posterior penetration to the caudal peduncle at 14,4 mm SL. The larval fishes commenced feeding at 5,35 mm NL. Pelvic buds formed between 6,9–7,2 mm SL. The larval fish transformed to juveniles by 13,0 mm SL.

Notes on the breeding behaviour, habitat preference and conservation of *S. capensis* are included.

INTRODUCTION

The early life history of *S. capensis* is poorly known, in fact there have been few studies on the early development of African anabantids (Cambray and Teugels, 1988).

Sandelia capensis is one of the freshwater fish species which is endemic to the Cape Fold Mountain region. The natural distribution of *S. capensis* is confined to the Cape Province where it occurs in most lowland and middle reaches of Cape rivers from the Coega River in the Eastern Cape to Verlorevlei and the Berg River in the South-Western Cape (Jubb, 1965; Gaigher et al., 1980). Hamman et al. (1984) reported an introduced population which had become established in a tributary of the Olifants River System in the Western Cape Province.

Sandelia capensis is capable of tolerating a wide variety of water conditions, both physical and chemical (Harrison, 1952). It is found in the upper reaches of clear, swift-flowing rivers, in intensely peat-stained acidic rivers, alkaline rivers, in heavily silted rivers, and muddy still

waters. Harrison (1952) also noted that it survives in very stagnant back-waters and cut-offs which are avoided by *Barbus* species and the exotic predators, trout and black bass.

The presence of *Sandelia*, which belongs to the primary division of freshwater fishes (see Hofmeyr, 1966) being completely isolated in the southern tip of Africa, is a zoogeographical puzzle (Jubb, 1967). The two anabantoid species, *Sandelia capensis* (Cuvier *in* C. and V., 1831) and *S. bainsii* Castelnau 1861 are unusual elements of the Cape ichthyofauna. The members of this family, which is considered to be the most primitive of the anabantoid families (Liem, 1963), are mainly distributed in tropical latitudes (Skelton, 1986). Liem (1963) considered that *S. capensis* was derived from the genus *Ctenopoma* that occurs in tropical Africa. However, Skelton (1986) considered that the phylogenetic relationships of the two *Sandelia* species required further study according to cladistic principles. S. Norris (in litt.) is examining the interrelationships of the African Anabantidae. At present the anabantid genus, *Sandelia*, is a biogeographically uninformative element in the southern African fauna (Skelton, 1986).

METHODS

Adult *S. capensis* were collected from a feral population in the Thomas Baines Nature Reserve near Grahamstown.

Sandelia capensis spawned in the aquarium, and developing embryos were collected from four separate spawning acts and each spawning was put into a separate rearing aquarium. The embryos were collected for observation, drawing and photographing at various stages of development. The early larval stages were fed live rotifers and sieved daphnia. Older larval fish were fed daphnia and a balanced flake food. The temperature in the rearing tanks was maintained at between 22 and 24 °C and one-third of the water was replaced every five days. The pH of the water was neutral to slightly alkaline (7,0–7,2).

Specimens were illustrated with the aid of a camera lucida and a binocular dissecting microscope. Eleven morphometric and seven meristic characters were measured or counted. Meristic characters included counts of preanal and postanal myomeres and caudal (principal and secondary), dorsal, pectoral and pelvic fin rays and spines.

Measurements of the smaller specimens were taken using an ocular micrometer in a dissecting microscope and larger specimens were measured with dial callipers (accuracy 0,05 mm). Measurements were made at least six months after preservation. All measurements in the text are from preserved material unless otherwise noted.

DEFINITION OF TERMS USED.

Lengths of specimens are reported as notochord length (NL) or standard length (SL) in mm unless otherwise stated. Total length (TL) is measured from the snout tip, through the horizontal body axis, to the end of the caudal finfold or a perpendicular to the end of the longest caudal fin ray. Standard length (SL) is measured from the snout tip, through the horizontal body axis to the end of the median bones at the caudal base. Standard length measurement is not accurate until the horizontal alignment of the median hypural bones is completed. Notochord length (NL) is measured from the snout tip of the notochord before its dorsal flexion, and afterwards perpendicular to the horizontal body axis through the tip of the upturned notochord (Berry and Richards 1973). Eye diameter (ED) is the maximum width of the eye measured on the horizontal axis. Head length is the horizontal distance from the snout to the posterior edge of the opercle. Preanal length (PL) is the distance from the snout to the origin of the anal fin, (in small larvae

before differentiation of the anal fin, the measurement was taken from the snout to the posterior edge of the anus). Head depth (HD) is the length of a vertical line immediately posterior to eye. Body depth at pectoral fin (BDp) is the depth of the body at pectoral fin base. Body depth at anus (BDa) is the depth of body at posterior edge of anus. Head width (HW) is the width of head immediately posterior to eyes. Body width at pectorals (BWp) is the width of the body at base of pectorals. Preanal myomeres are all those segments of which their bordering myosepta are at least partly anterior to the anus including one segment anterior to the first myoseptum. Postanal myomeres are all those segments posterior to preanal myomeres including a urostylar segment (Fuiman, 1982). Myomeres were counted with the aid of polarizing filters. Myomeres of large opaque specimens were not counted because of lack of clarity.

Embryos and larvae were preserved in a 5% phosphate-buffered formalin solution after being tranquillized with benzocaine to relax specimens and reduce curvature during fixation.

The surface of the egg envelope was viewed, up to a magnification of 6 000×, using a JEOL JSM 840 Scanning Electron Microscope operating at 10 kV. The eggs had been preserved in 5% phosphate buffered formalin. The eggs were prepared for SEM work by standard procedures, alcohol dehydration and critical point drying. The samples were mounted on aluminium stubs and coated with a thin layer of gold in a sputtering device. Several eggs were also prepared using the Cryo technique, which involves freezing the eggs in liquid nitrogen, coating with gold and then viewing.

A population of *S. capensis* in the Wit River, a clear, slightly acidic (pH 6,6–6,9), Cape Fold Mountain tributary of the Gamtoos River System, was observed and early life history stages were collected. The habitat of these early stages was recorded.

All specimens have been catalogued (AMG/P 12245) in the Ichthyological Collection of the Albany Museum, Grahamstown.

RESULTS

FERTILIZATION

The exact time of activation was not known. Eggs were removed from the male's nest and transferred to a rearing aquarium, after they had been fertilized naturally in the breeding tank.

EGG DESCRIPTION

Ripe unshed eggs were pale yellow in colour with a mean diameter of 1,1 mm (SD = 0,05 mm, n = 25). Water-hardened *S. capensis* eggs were strongly adhesive and negatively buoyant. The outer egg envelope remained strongly adhesive until the free embryos hatched. The water-hardened eggs were 1,28 mm (SD = 0,08 mm, n = 31) in diameter and were initially crystal clear in colour, mainly round, as only 9 out of 31 measured eggs were slightly elliptical. Therefore the swelling of the egg membrane was minimal (0,18 mm) or 14% of the diameter of the shed fertilized egg. A single oil globule measuring 0,62 mm (SD = 0,04 mm, n = 31) was suspended in the yolk (Fig. 1a). When the eggs were artificially released from their adhesive contact the oil globule was not large enough to give positive buoyancy to the eggs. Surface tension was sufficient to keep the eggs buoyant but if the surface tension was broken the eggs sank.

The egg envelope remained highly adhesive until the free embryos hatched. Some of the free embryos remained connected to the broken egg envelope (Fig. 5a) which could be seen on the aquarium gravel to which the developing embryo had been attached.

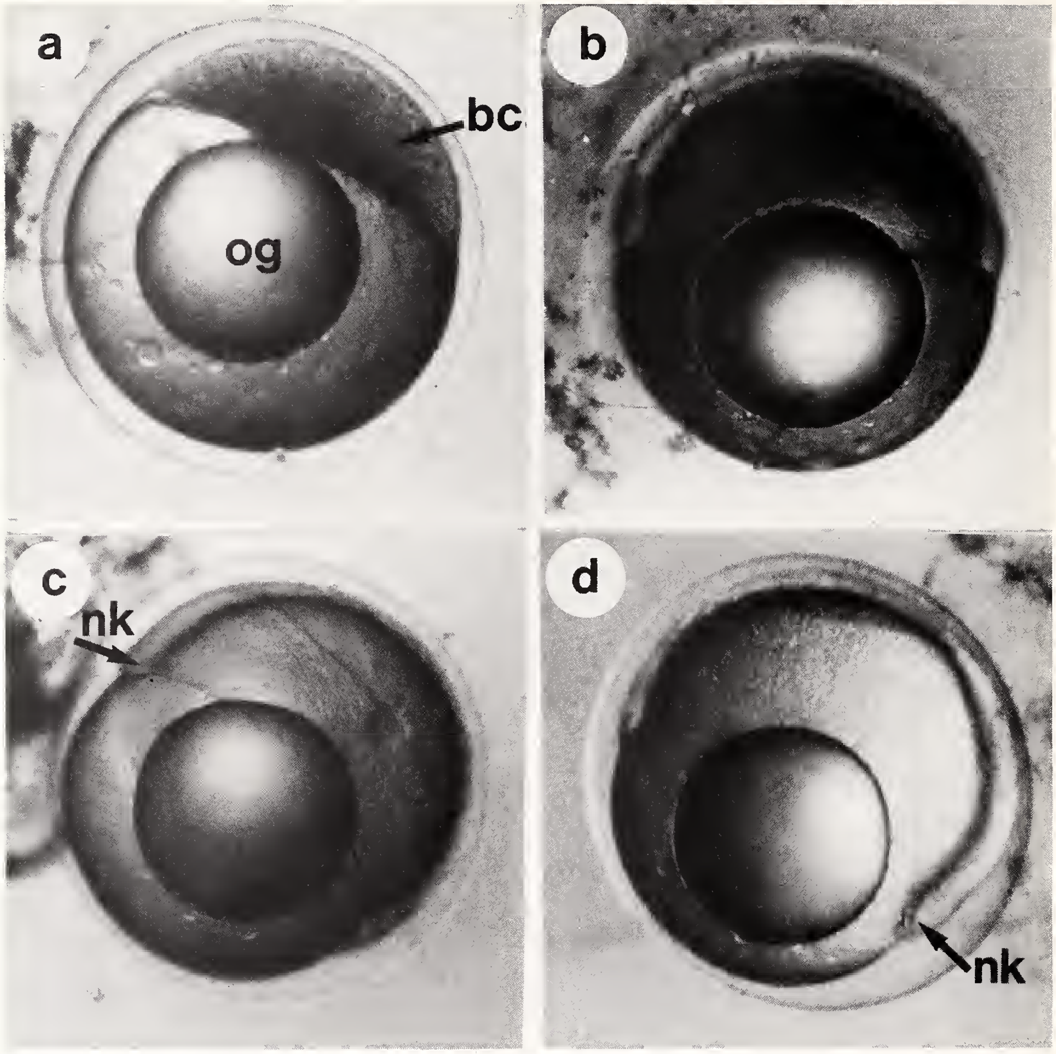

Fig. 1. Several early embryonic stages of *Sandelia capensis*. All ages given are calculated from time of first egg collection, which is the egg shown in (a). (a) Blastodermal cap, age 0 h. (b) Equatorial position, age 3,5 h. (c) Age 4,5 h. (d) Neural keel, age 6,5 h. All the eggs are between 1,0 and 1,4 mm in diameter. bc–blastodermal cap; nk–neural keel; og–oil globule.

The ultrastructure of the egg envelope of *S. capensis* was viewed up to a magnification of 6 000× and only a faint ultrastructural patterning was observed (Fig. 3). The egg envelope of *S. capensis* was therefore fairly smooth with round markings and a central raised structure. The Cryo treated material gave the best results.

EMBRYONIC DEVELOPMENT

On the 24–01–1985 between 14h00 and 15h00 one male *S. capensis* started to chase a female. At this time petri dishes were put in the nesting area of the male and at 17h00, water temperature 23 °C, several eggs were found in one of the petri dishes. The eggs were examined and found to be in a many-celled blastodermal cap stage (Fig. 1a). The cells were opaque and the yolk was clear.

The blastoderm was in equatorial position after 3,5 h (Fig. 1b). The neural keel was evident after 4,5 h (Fig. 1c) and after 6,5 h the neural keel was a dominant feature of the developing embryo (Fig. 1d). The oil globule within the yolk made it very difficult to orientate the developing embryo for observation and photographing. After 14 h from collection time the optic cups and Kupffer's vesicle had formed (Fig. 2a). Somites and pigment were first observed after 16,5 h (Fig. 2b). The black pigment became a dominant feature of the developing embryo after this stage and obscured some of the embryonic development. The pigment developed as large irregular 'blotches' on the embryonic head and over the surface of the yolk (Fig. 2c). After 22 h the eye lens was forming and the somites almost reached to the tail tip (Fig. 2c). Muscular contractions were first seen after 24 h (the heart-beat stage), also the otic placode had just started to form (Fig. 2d).

At 26 h the circulatory system had developed over the surface of the yolk and under the notochord. After 30 h otoliths were observed and approximately 20% of the tail was free from the yolk-sac, the heart beat was 112 (SD = 4, n = 3). After 32 h the tail overlapped the head and the embryo was now actively twisting and revolving in the egg envelope.

After 40,5 h the first free embryo hatched (3,1 (3,0) mm TL (NL), alive) (Fig. 4a). When the free embryos were released from their adhesive attachment they could swim for approximately 15 seconds in a spiralling upward movement. After this active period they stopped and passively sank and readhered to either the glass or the aquarium gravel. The heart-beat had lowered from 123 (SD = 6, n = 3) just prior to hatching to 104 (SD = 10, n = 3) at hatching. After 42,5 h, seven of the 16 developing embryos had hatched.

FREE EMBRYOS AND LARVAL *S. CAPENSIS*

Lengths given are those at which the initial formation of selected structures occurred. AL = alive, P = preserved measurements. After 40,5 h at between 22–23 °C the first free embryo hatched (3,1 (3,0) mm TL (NL) AL) (Fig. 4a). Including the results from all spawnings newly hatched free embryos were 3,47 mm NL (L) (3,0–3,6 mm NL, SD = 0,15, n = 13), with a single oil globule 0,65 mm in diameter (SD = 0,08) positioned antero—ventrally in the yolk sac. The dorsum of the head was adhesive (Fig. 4b). When the free embryo became attached to an object possibly the buoyancy of the oil globule resulted in the ventral surface of the free embryo being uppermost (Fig. 5a). The newly hatched free embryos had 8–9 preanal and 17–18 postanal myomeres (Table 1). The head remained deflected ventrally over the anterior margin of the yolk sac (Figs 5b and c) until *c* 4,6 mm NL (L) and during this period the oil globule migrated posteriorly (Fig. 6a). The pectoral fin buds were present at 4,35 mm NL and the swimbladder first inflated at *c* 4,8 mm NL (P) (Fig. 6b). Functional mouthparts formed at

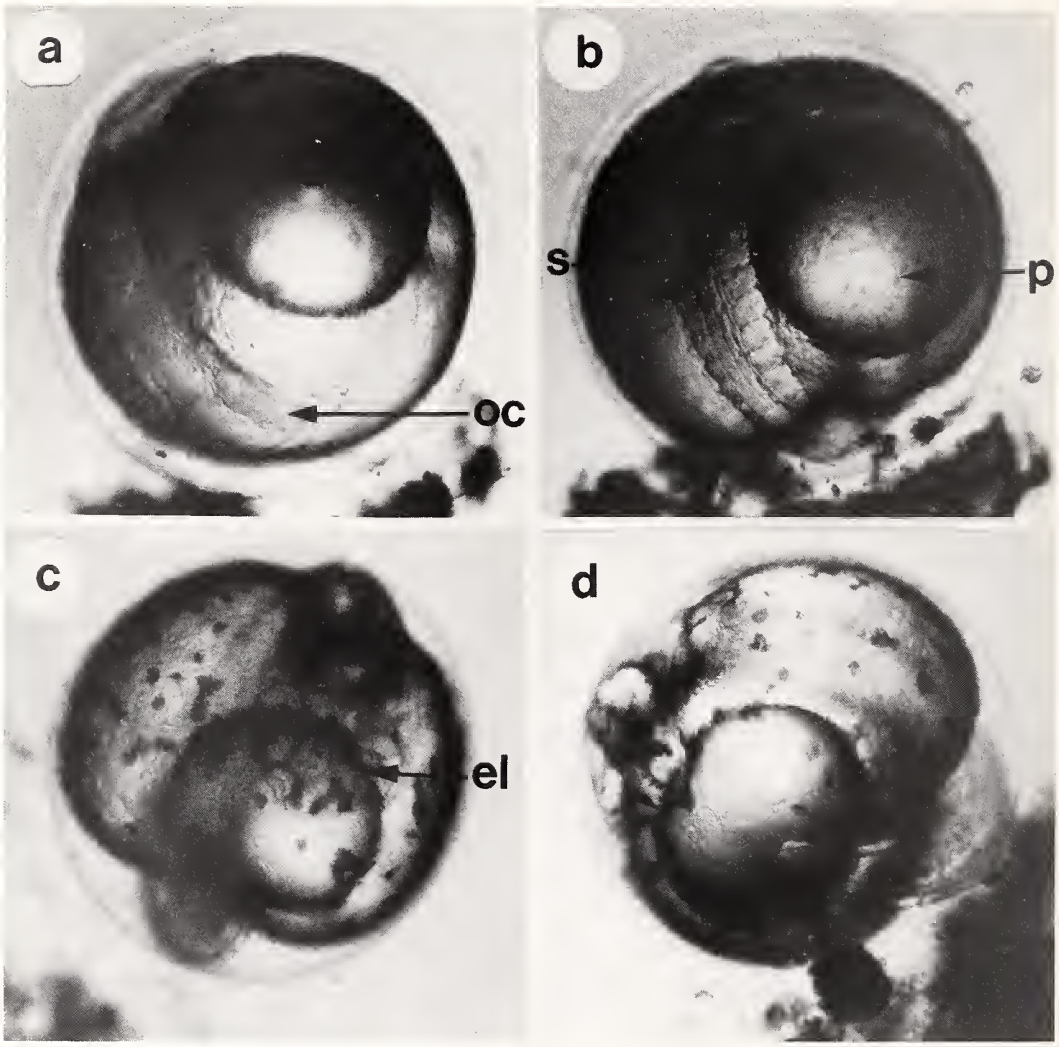

Fig. 2. Several early embryonic stages of *Sandelia capensis*. All ages given are calculated from time of first egg collection, which is the egg shown in Fig. 1(a). (a) Optic cups forming, age 14 h. (b) and (c) Somite formation and commencement of pigmentation, age 16,5 h. (d) Heart-beat stage, age 24,5 h. All the eggs are between 1,0 and 1,4 mm in diameter. el–eye lens; oc–optic cup; p–pigment; s–somite.

c 4,8 mm NL (P). The bluish-gray coloured oil globules divided into left and right globules at *c* 4,7–4,92 mm NL. These globules moved dorsally (Figs 9a-e) and came to lie in a position flanking the developing swimbladder (Figs 6c, 7a and 9e). The paired oil globules were asymmetrical (Fig. 9d). The oil globules disappeared at between 6,3–6,9 mm NL. The yolk was absorbed at *c* 5, 1–5,3 mm NL and the larval fish first commenced feeding at *c* 5,4 mm NL (alive), (5,35 mm NL preserved). Notochord flexion commenced at *c* 6,2 mm NL (P) (Fig. 7b) and was completed at *c* 6,9 mm SL (P). The caudal finfold exhibited a transitory dorsal lobe (Fig. 8a) which formed at *c* 6,9 mm NL (P) and this lobe disappeared at *c* 6,9 mm SL (P) when the caudal fin was now rounded (Fig. 8b).

The incipient dorsal fin margin was partially differentiated at 6,5 mm NL (P) and completely differentiated at 8,2 mm SL (P). The dorsal fin origin was over myomeres 3–4. The first dorsal rays formed at 7,0 mm NL (P). Theincipient anal fin margin was partially differentiated at 6,9 mm NL (P) and completely differentiated at *c* 8,6 mm SL (P). Anal and

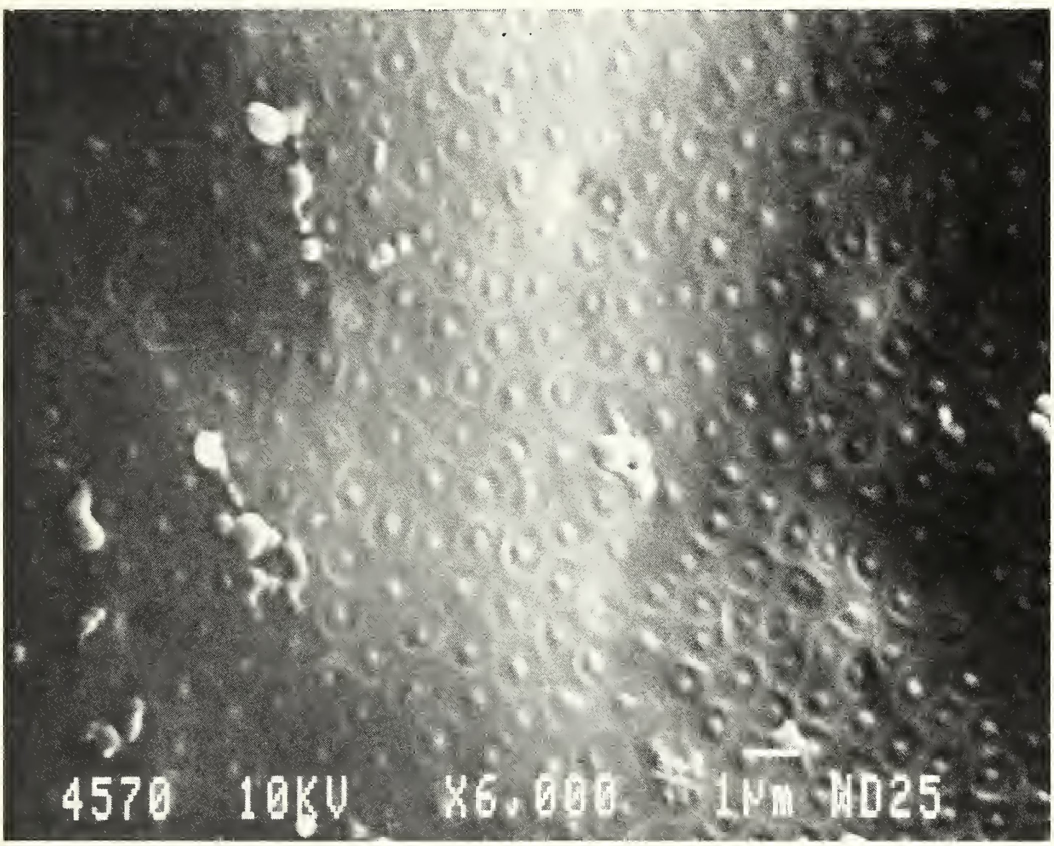

Fig. 3. Egg envelope ultrastructure of *Sandelia capensis*. Scale bar = 1 μm.

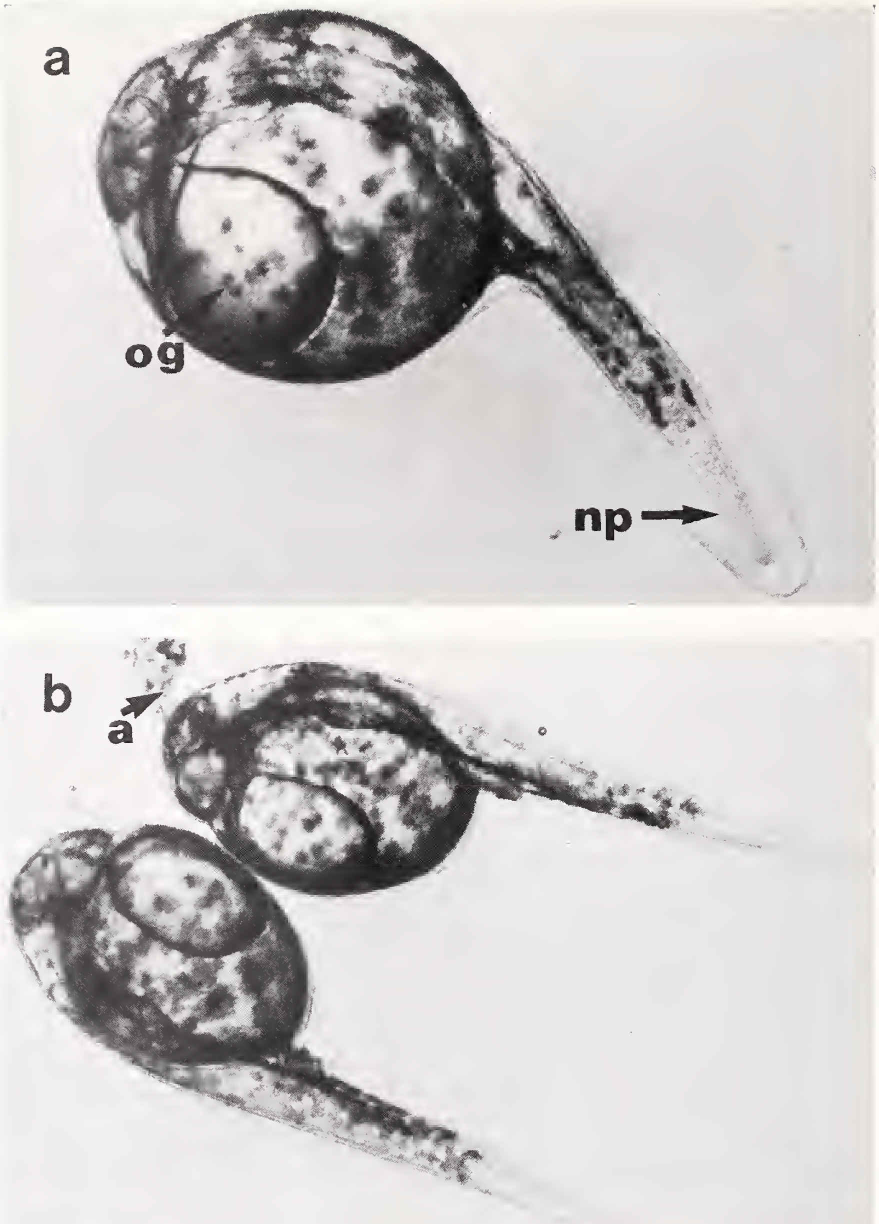

Fig. 4. Post hatching developmental stages of *Sandelia capensis*. All measurements are for live fish. (a) Newly hatched free embryo, 3,1 (3,0) mm TL (NL). (b) Two recently hatched free embryos, (top 3,5 (3,4) mm TL (NL) and 3,7 (3,6) mm TL (NL)). a–adhesive material; np–no pigment; og–oil globule.

TABLE 1

Meristic characters of 118 *Sandelia capensis* free embryos, larvae and juveniles used in the present developmental description.

Length interval	n	Myomeres			Caudal fin rays				Dorsal fin rays	Anal fin rays	Pelvic fin rays	Pectoral fin rays
NL or SL (mm range)		Preanal	Postanal	Total	Dorsal secondary	Dorsal principal	Ventral secondary	Ventral principal				
3 (3,4–3,8)	8	8–9	17–18	25–26	0	0	0	0	0	0	0	0
4 (4,0–4,9)	23	7–10	15–17	23–27	0	0	0	0	0	0	0	0
5 (5,1–5,8)	12	8–11	15–17	25–28	0	0	0	0	0	0	0	0
6 (6,2–6,9)	9	10–12	14–17	25–28	0	7–8	0	7–9	0–6	0–8	0	0
7 (7,0–7,3)NL	6	10–11	15–17	26–28	0	8	1	7–8	0–6	0–8	0	0–9
7 (7,0–7,8)SL	12	12–14	14–15	27–28	0	8	0–2	8	4–18	8–14	fin buds	7–10
8 (8,0–8,6)	8	opaque	opaque		2–3	8	2–3	8	15–22	14–16	fin buds	10–14
9 (9,0–9,95)	6	opaque	opaque		2–3	8	2–3	8	xii-xiii + 7–8	vii-viii + 7–9	0–3	8–14
10 (10,1–10,75)	8	opaque	opaque		3	8	3	8	xii-xiii + 8–9	vii-viii + 8–9	3–6	9–13
11 (11,0–11,9)	4	opaque	opaque		2–4	8	3–4	8	xiii + 8–9	vii-viii + 8	3–5	11–14
12 (12,18–12,71)	2	opaque	opaque		3–4	8	3–4	8	xiii + 8–9	vii-viii + 8	3–5	10–13
13 (13,0–13,9)	3	opaque	opaque		3–4	8	3–4	8	xii-xiv + 8	vii-viii + 7–8	6	11–12
14 (14,37–14,4)	3	opaque	opaque		3	8	3	8–9	xi-xiii + 8–9	vii-viii + 8	i + 5	11–13
15 (15,24)	1	opaque	opaque		3	8	3	9	xiii + 9	viii + 8	i + 5	14
16 (16,03–16,8)	3	opaque	opaque		3	8	3	8–9	xiii + 8	viii + 8	i + 4–5	13
18 (18,06)	1	opaque	opaque		3	8	3	8	xiii + 8	viii + 8	i + 5	12
19 (19,13–19,24)	2	opaque	opaque		3	8	3	8	xiii + 8	viii + 8	i + 5	14

TABLE 2

Proportional measurements relative to notochord or standard length for 118 *Sandelia capensis* free embryos, larvae and juveniles. Fish are grouped by 1 mm intervals of notochord (NL) or standard length (SL) (n = sample size). ED = eye diameter, HD = head depth, BDp = body depth at pectorals, BDa = body depth at anus, HW = head width, BWp = Body width at pectorals.

n	NL or SL (mm)	TL (mm)	TL:SL	Preanal: SL	Snout:SL	Head:SL	ED:SL	HD:SL	BDp:SL	BDa:SL	HW:SL	BWp:SL
8	3,58+0,23	3,67+0,26	1,03	0,56	0,05	—	0,1	0,09	0,32	0,094	0,171	0,28
23	4,6 +0,27	4,76+0,28	1,035	0,477	0,023	0,223	0,098	0,071	0,236	0,135	0,167	0,171
12	5,44+0,26	5,62+0,25	1,034	0,465	0,042	0,239	0,106	0,212	0,213	0,15	0,175	0,133
16	6,6 +0,34	6,85+0,41	1,037	0,486	0,048	0,26	0,109	0,227	0,167	0,184	0,188	0,162
6	7,13+0,13	7,68+0,26	1,076	0,5	0,058	0,284	0,116	0,235	0,255	0,201	0,194	0,164
12	7,35+0,27	9,09+0,42	1,237	0,584	0,069	0,343	0,134	0,279	0,31	0,261	0,222	0,198
8	8,39+0,31	10,58+0,47	1,261	0,594	0,074	0,359	0,14	0,295	0,324	0,292	0,234	0,21
6	9,38+0,37	11,82+0,46	1,26	0,602	0,073	0,362	0,137	0,291	0,331	0,297	0,224	0,204
8	10,28+0,3	13,17+0,43	1,281	0,601	0,071	0,372	0,14	0,295	0,342	0,315	0,234	0,212
4	11,57+0,4	14,81+0,53	1,28	0,604	0,081	0,385	0,127	0,296	0,365	0,332	0,147	0,223
2	12,45+0,38	15,71+0,59	1,26	0,6	0,082	0,365	0,283	0,212	0,337	0,307	0,147	0,209
3	13,52+0,47	17,33+0,73	1,28	0,616	0,075	0,382	0,116	0,3	0,37	0,242	0,152	0,219
3	14,38+0,02	18,41+0,07	1,28	0,605	0,079	0,38	0,131	0,287	0,362	0,327	0,227	0,223
1	15,24	19,32	1,27	0,617	0,085	0,387	0,125	0,295	0,381	0,361	0,223	0,236
3	16,31+0,43	20,76+0,56	1,273	0,602	0,08	0,387	0,128	0,285	0,373	0,347	0,227	0,227
1	18,06	23,23	1,286	0,609	0,083	0,396	0,127	0,291	0,365	0,338	0,216	0,216
2	19,19+0,78	24,76+0,43	1,29	0,612	0,081	0,378	0,122	0,281	0,362	0,331	0,211	0,234

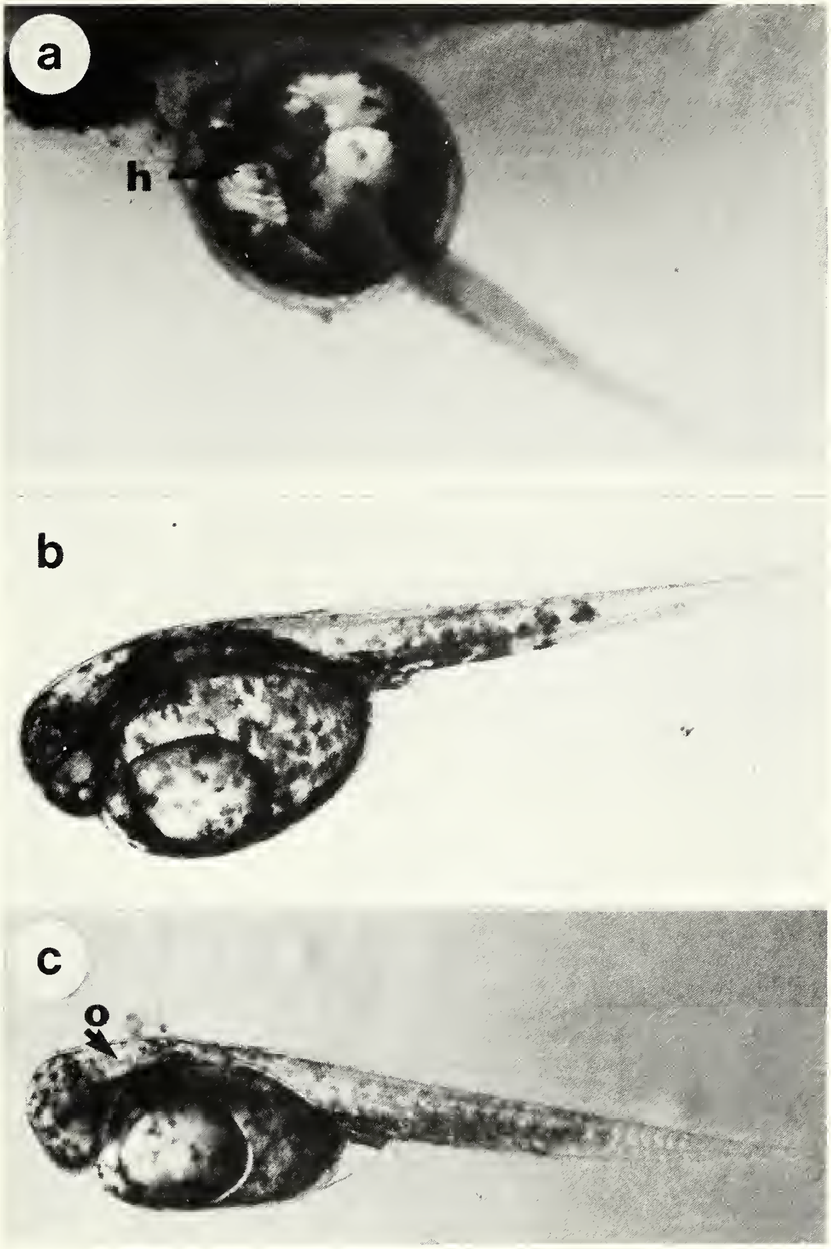

Fig. 5. Post hatching developmental stages of *Sandelia capensis*. All measurements are for live fish. (a) In situ dorsal view of a 3,1 mm TL free embryo. (b) Free embryo, age 53,5h, 4,1 (4,0) mm TL (NL). (c) Free embryo, 4,1 (4,0) mm TL (NL). h–head; o–otolith.

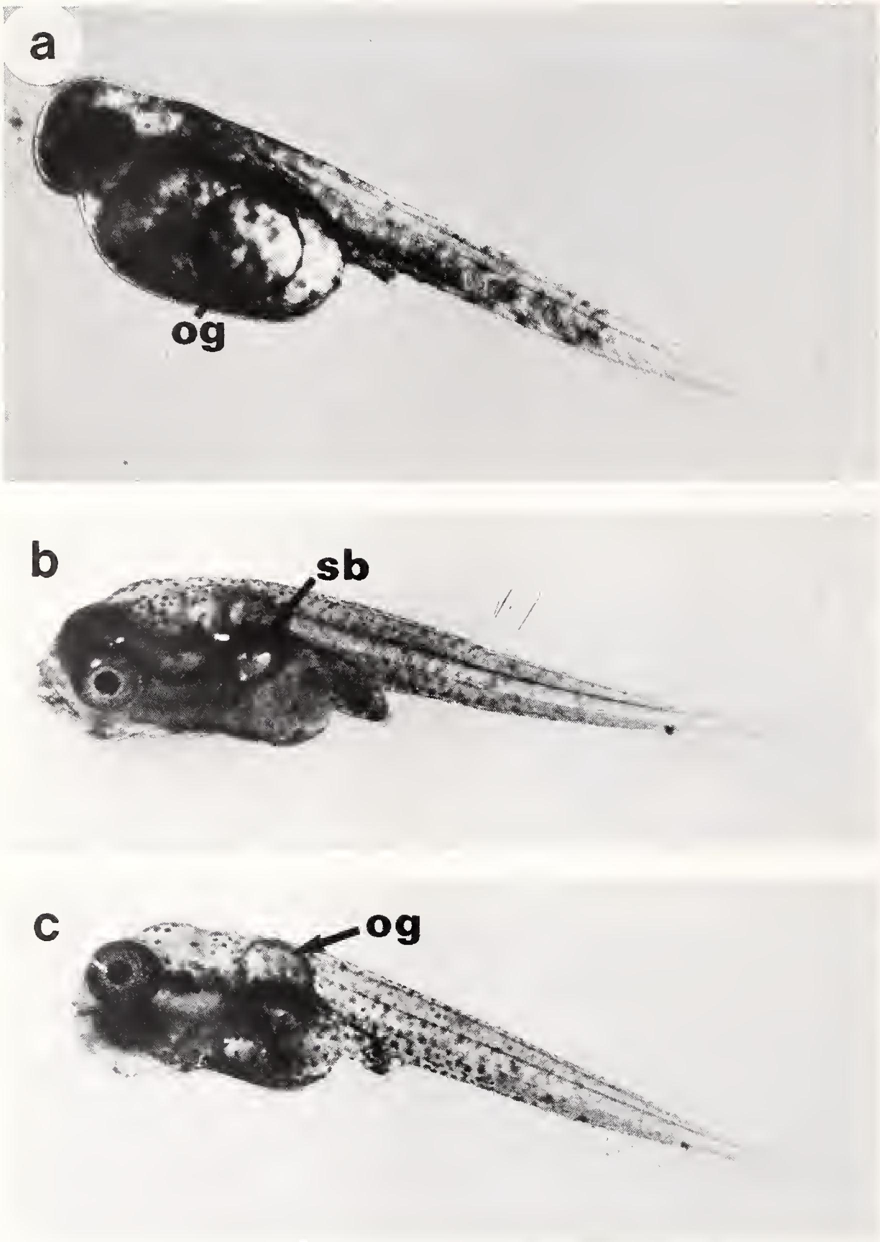

Fig. 6. Post hatching developmental stages of *Sandelia capensis*. All measurements are for live fish. (a) Free embryo, 4,7 (4,6) mm TL (NL). (b) Larval fish, 5,0 (4,9) mm TL (NL). (c) Larval fish 5,2 (5,0) mm TL (NL). og–oil globule; sb–swimbladder.

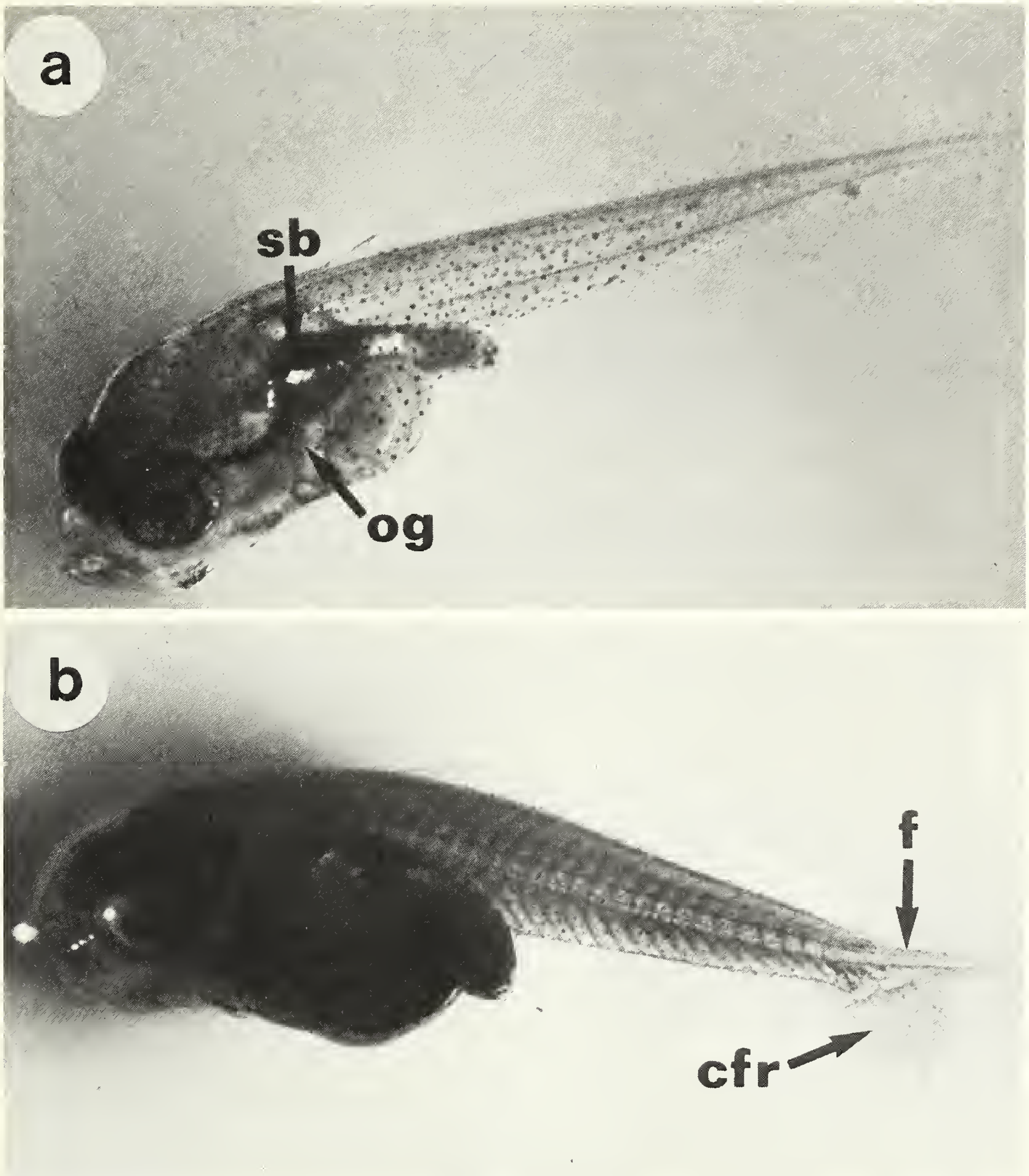

Fig. 7. Post hatching developmental stages of *Sandelia capensis*. All measurements are for live fish. (a) Larval fish 5,8 5,7) mm TL (NL). (b) Flexion, larval fish 7,3 (7,0) mm TL (NL). cfr–caudal fin ray; f–flexion; og–oil globule; sb–swimbladder.

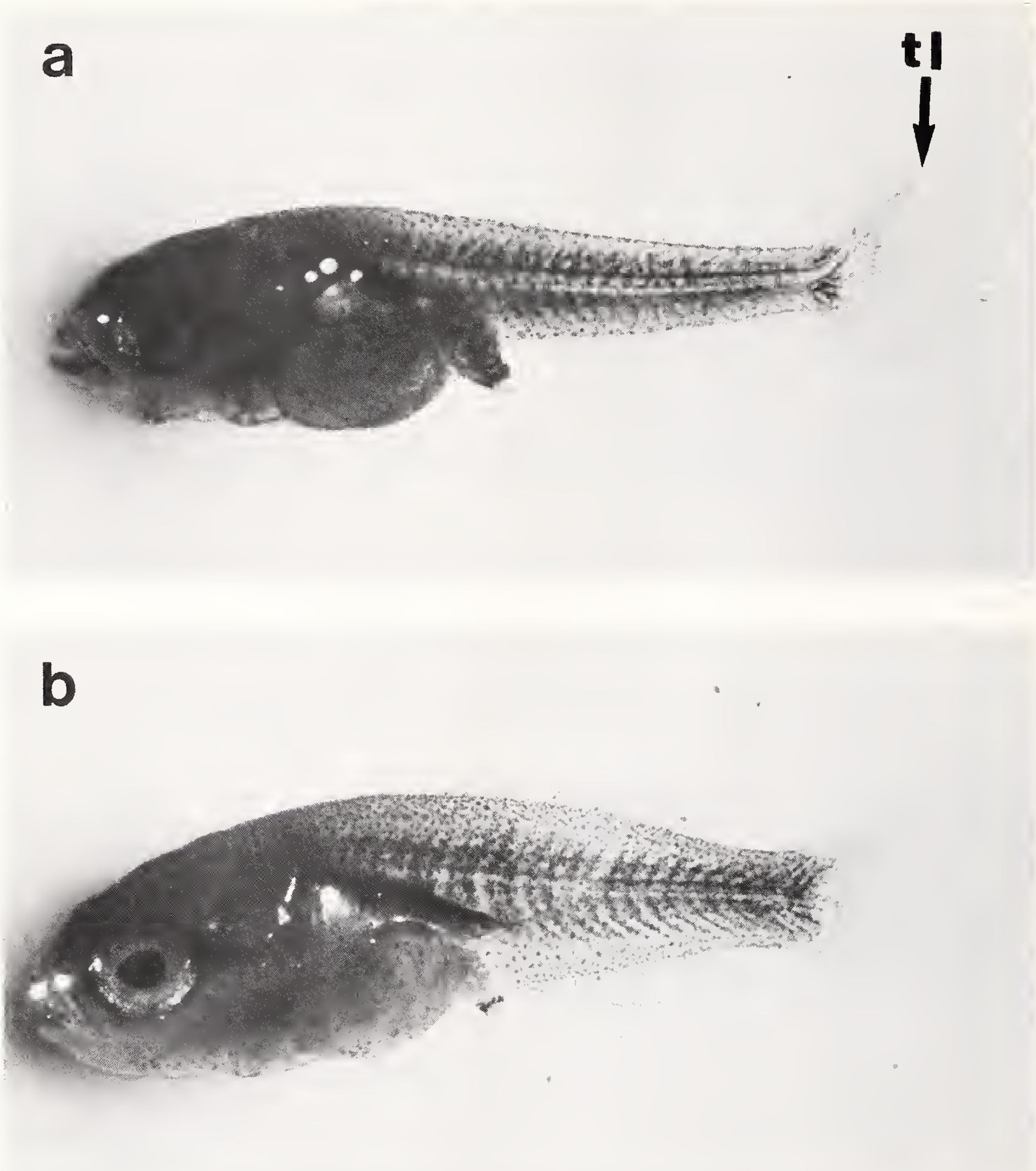

Fig. 8. Post hatching developmental stages of *Sandelia capensis*. All measurements are for live fish. (a) Transitory caudal fin lobe, larval fish, age 21,2 days (23 °C), 7,7 (6,2) mm TL (SL). (b) Late larval fish, 8,8 (6,9) mm TL (SL). tl–transitory lobe of the caudal fin.

dorsal fin rays commenced branching at 8,6 mm SL (P). The pelvic buds formed at *c* 6,9–7,2 mm SL (P) and the first pelvic rays were seen in a 9,2 mm SL (P) specimen. The entire finfold was absorbed at 11,74 mm SL (P). Squamation began between 9,0–9,5 mm SL (P).

OIL GLOBULE DESCRIPTION

Each early free embryo had only one oil globule (Figs 4a and 9a). This oil globule and its position (Fig. 4b) are probably the reasons why free embryos lie with their ventral surfaces positioned upwards (Fig. 5a). The bluish oil globule begins to move posteriorly (Fig. 6a) and then dorsally at *c* 4,7 mm NL (P) (Figs 9b and c) and by 4,95 mm NL (P) there are distinct left and right oil globules (Fig. 9d). This movement of the oil globule coincides with the inflation of the swimbladder (Fig. 6b). In some specimens it was observed that the oil globule on one side divided into an upper and lower globule (Fig. 9e). There appeared to be variability in the size of the oil globules and the right side is usually the larger of the two (Fig. 9d). Oil globules disappeared in specimens between 6,3 and 6,9 mm NL (P), a stage at which the swimbladder was well developed.

SWIMBLADDER DEVELOPMENT

The swimbladder first inflated at *c* 4,8 mm NL (P) (Fig. 6b). At 6,25 mm NL (P) (estimated 6,3 mm SL) the swimbladder started to project posteriorly and at *c* 8,7 mm SL (P) (Fig. 10a) the swimbladder had completed its extension over the gut and now commenced to extend posteriorly under and parallel to the vertebral column. This posterior elongation of the swimbladder is completed at *c* 14,4 mm SL (Fig. 10b) when the swimbladder touches the hypural plates. The development of the swimbladder for several specimens of different ages can be seen in Fig. 11. The relationship of this posterior prolongation of the swimbladder relative to notochord or standard length is shown in Fig. 12.

PIGMENTATION

Pigmentation commences on the embryonic yolksac (Fig. 2c). The pigmentation has the form of irregular spots which occur randomly over the yolksac surface and on the developing embryo (Fig. 2d). Pigment on the newly hatched free embryo occurs on the yolksac and body except for the posterior tip of the body, 0,8 mm from the posterior tip of the caudal finfold (Fig. 4a). The pigment is very variable in size and shape. This pigment pattern is also visible on a free embryo of 4,1 mm TL (Fig. 5c).

At 4,7 mm TL the fish still have a clear unpigmented posterior tip to their bodies. The eye is heavily pigmented and the rest of the body is covered with black pigment spots, but no pattern is obvious (Fig. 6a).

At 5,2 mm TL the dorsal half of the body is yellow and some black pigment now occurs on the posterior tip of the body. There is also pigment on the dorsal and ventral finfolds. There is still no distinct pattern, however, pigment spots are now relatively smaller and darker, especially noticeable on the dorsum of the head (Figs 6b and 6c).

At 7,7 mm TL the pigment spots are finer and the entire body is peppered with these pigment spots (Fig. 8a). On the dorsal fin the first large dark pigment spot is evident at the posterior of the dorsal fin and the rays in the dorsal fin are outlined with pigment at 10,0 mm TL (7,9 mm SL). The finer peppering continues until at *c* 12 mm TL the dorsal to ventral body

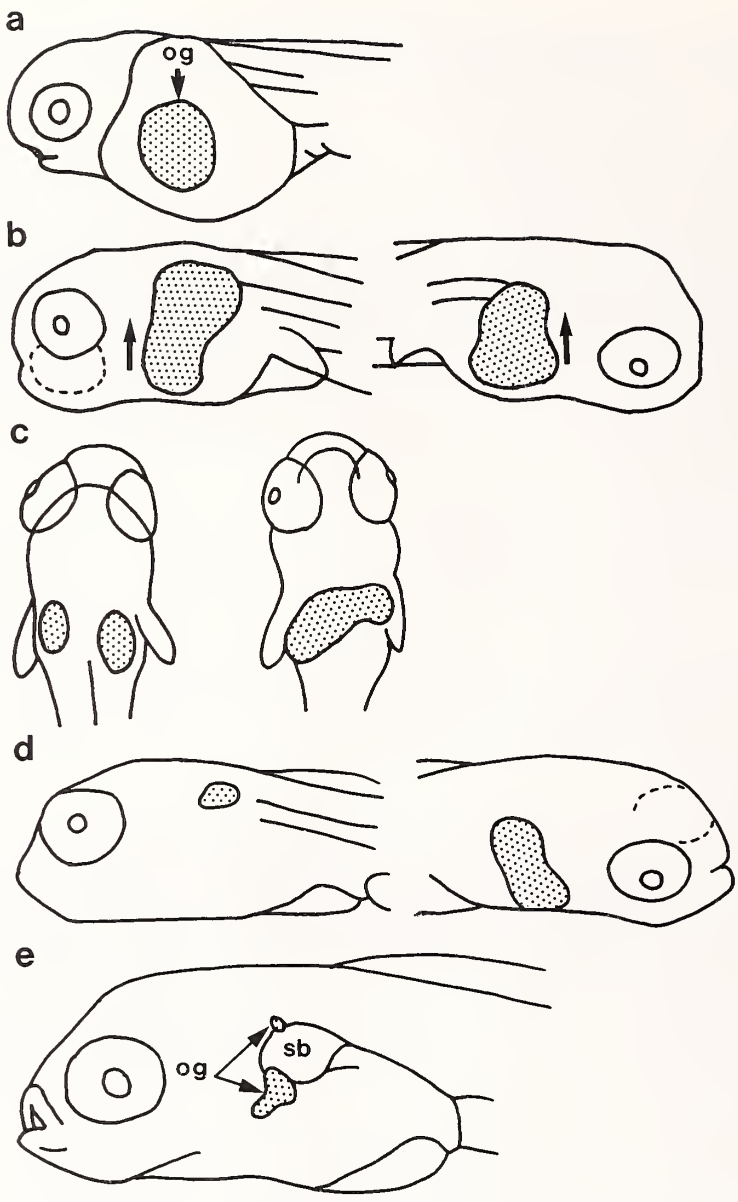

Fig. 9. Oil globule movement during the development of *S. capensis*. All measurements refer to preserved material. (a) Position of the single oil globule in a recently hatched free embryo, 4,75 (4,6) mm TL (NL). (b) Movement of the oil globule dorsally, left and right views of a 4,9 (4,7) mm TL (NL) free embryo. (c) Dorsal and ventral views of the migrating oil globule of a 4,9 (4,7) mm TL (NL) free embryo. (d) Two separate asymmetrical oil globules in a 5,1 (4,95) mm TL (NL) individual. (e) The oil globule on the left has dispersed into two separate globules in a 6,6 (6,4) mm TL (NL) fish. og = oil globule, sb = swimbladder, arrows in (b) indicate movement of the oil globule.

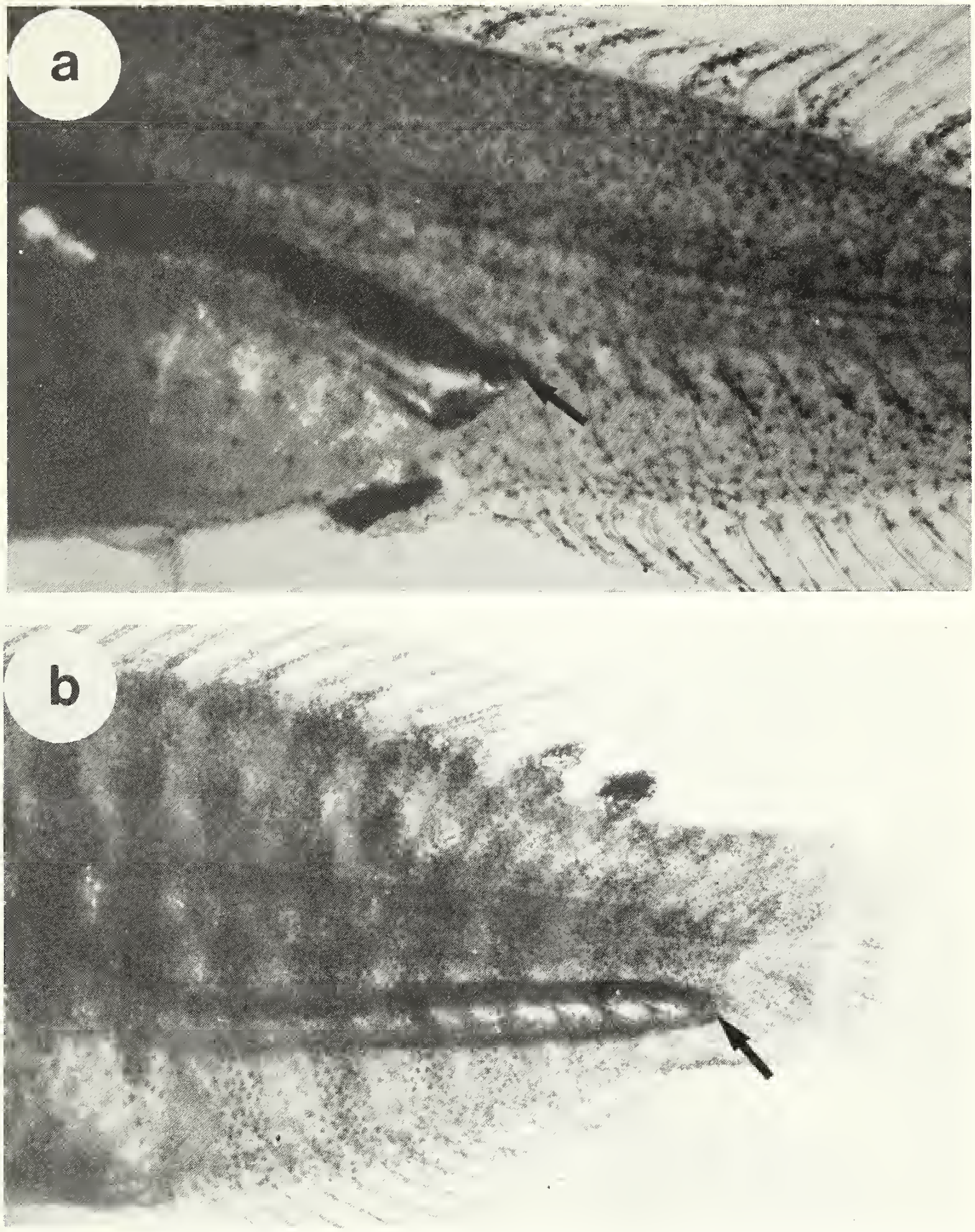

Fig. 10. (a) Close-up of the beginning of the posterior prolongation of the swimbladder parallel to the vertebral column in a 11,0 (8,78) mm TL (SL) *S. capensis*. (b) Close-up of the maximum posterior prolongation of the swimbladder in a 18,2 (14,4) mm TL (SL) *S. capensis*. All measurements are from live material. Arrows indicate the posterior tip of the posterior prolongation.

stripes begin to appear which are characteristic of the juvenile fish as shown in Fig. 11 for a 13,8 mm TL (10,8 mm SL) specimen.

EARLY FREE EMBRYO AND LARVAL BEHAVIOUR

After hatching some of the free embryos remained attached for up to 10 h to the same rocks to which the eggs had adhered (Fig. 5a). Other free embryos were active and swam upwards to the surface and then sank passively. After this period when the rocks were lifted the embryos would come off and rapidly swim away. Three days post-hatch, at a size of *c* 5 mm TL, the embryos had moved away from the rocks (substratum) they had been attached to since hatching. Some of the free embryos hid between the gravel on the substratum of the nursery tanks, others were seen against the side of the tank hanging vertically with the dorsum of their heads in contact with the glass. Some fish swam ventral side up and only stopped when their heads touched an object in the tank. Others swam to the surface and 'butted' at the surface until they attached themselves to the surface tension. As soon as the surface tension was broken the young fish sank in a spiralling fashion. After four days from hatching the young fish started to feed on brine shrimp. The larval fish remain motionless, then take short (2–5 cm) dashes. Once they were near

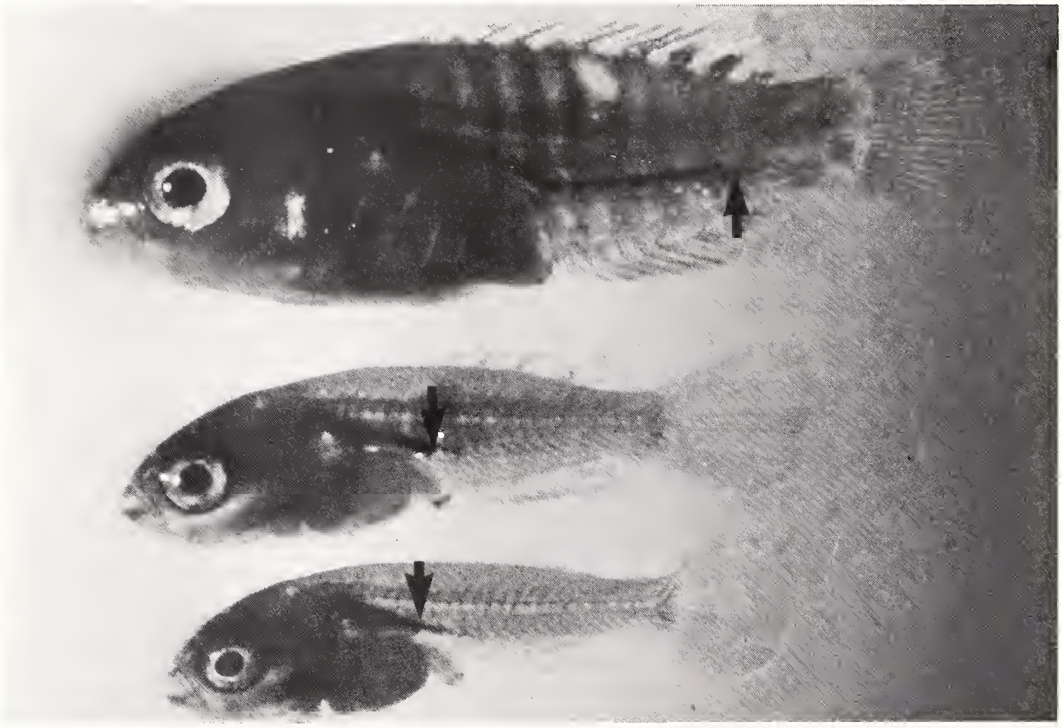

Fig. 11. Posterior prolongation of the swimbladders in several different age groups of *S. capensis*, from the top, 13,8 (10, 8), 9,7 (7,3), 8,8 (6,9) mm TL (SL). All measurements are from live material. Arrows indicate the posterior tip of the posterior prolongation.

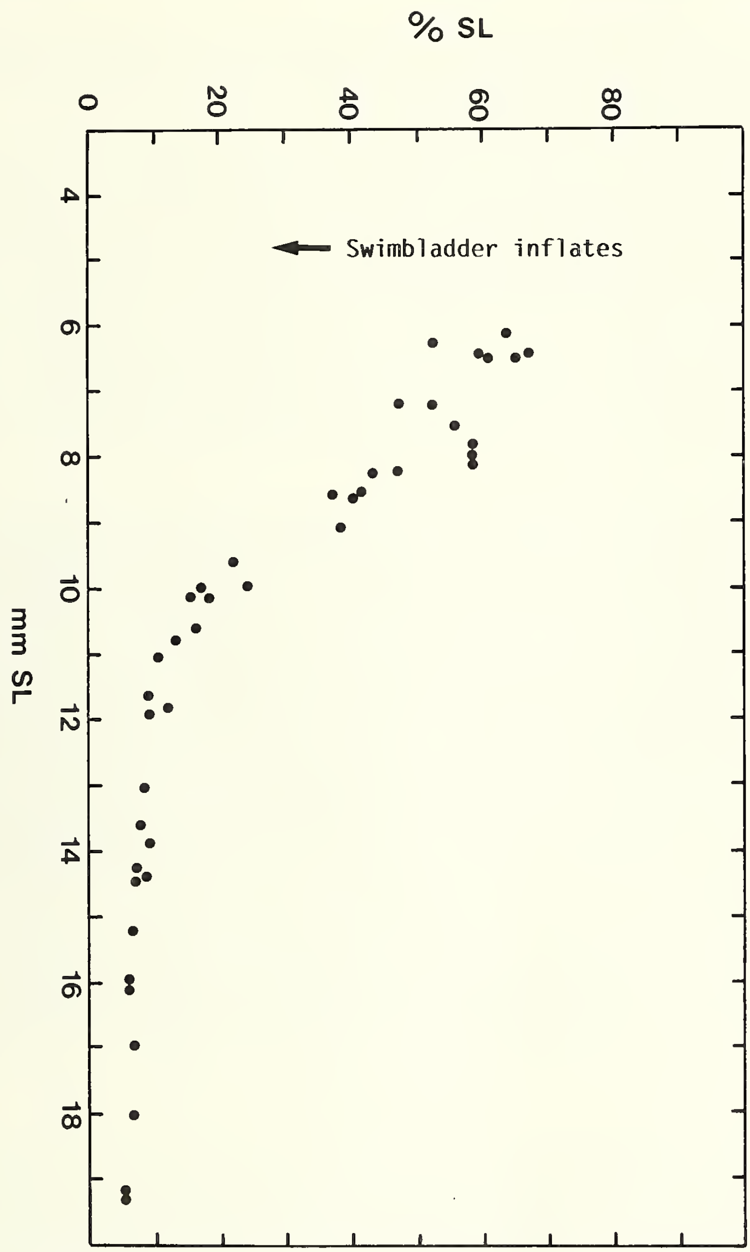

Fig. 12. The relationship of the distance from the tip of the posterior prolongation of the swimbladder to the tip of the notochord or the posterior edge of the hypural plates to notochord or standard length during the development of the swimbladder in *S. capensis*.

a prey item they manoeuvred within a few millimetres, maintained position, observed the prey, then darted forward and if successful swallowed the item. At this stage the larval fish have a swimbladder and can maintain themselves parallel to the surface of the water, and swim and behave in a manner similar to that of adults.

The arcing behaviour, as defined in Tooker and Millar (1980), which is characteristic of *S. capensis* adults (pers. obs.), was first observed in 5,0 mm NL fish, when the swimbladder had just inflated and the oil globule was moving from its ventral position to a position flanking the swimbladder (Fig. 9d). They arc (lateral bending) their caudal area and maintain a position while sculling with the large pectoral fins. When live prey items were given to the larval fish they swam within a few millimetres of the item, arc, observed and then dashed forward and tried to swallow the prey item. In many cases when the prey did not move the young fish ignored the item and swam away. The adult male was still guarding the young at this stage. After approximately 6,7 mm TL the larval fish were mainly on or near the substratum. Aggression was first noted when the fish were 15,0 mm TL. They turned a darker colour and chased siblings, in some cases killing them. The 15,0 mm TL specimen was able to kill fish of 10,9 and 13,8 mm TL.

FIELD OBSERVATIONS

Field observations of a population of *S. capensis* in the Wit River showed that fish were actively breeding during the middle of November 1988 when water temperatures were around 20–23 °C. Several small (*c* 15 cm TL) males, in breeding colours, were chasing females in small circles, however, no actual spawning was observed. The darkened males readily chased away any other sexually active males and, in this case, the chase was usually in a straight line until the chased fish found cover. Chase distances were usually less than three metres.

Diving observations revealed that the larger males, some as big as 20 cm TL, were occupying territories between tree roots where the river had eroded the bank. The tree roots as well as the open gravel area occupied by the smaller males were examined for eggs but no eggs were found. The following month (19-xii-1989) young-of-the-year *S. capensis* were collected amongst the submerged roots of Bushman's rhubarb (*Gunnera perpensa*). These fish were between 7,8 (7,4) and 13,48 (10,8) mm TL (SL) (n=17) (P). The smallest was a larval fish and flexion had just commenced. Minimum-maximum water temperatures between the two observational periods were 16,5–20,5 °C. These temperatures were recorded at a water depth of 80 cm with a min.-max. thermometer which was left in the water between monthly sampling periods. At the next sampling period (22-i-1989) young-of-the-year *S. capensis* in this area ranged in size from 8,2 (7,0)–15,44 (12,22) mm TL(SL) (n=19) (P). The range in size and developmental stages would indicate that several separate spawnings had taken place during the summer months. The largest fish (15,44 mm TL) still had a remnant of a preanal finfold.

DISCUSSION

EARLY LIFE HISTORY

Very little work has been done on the early life history of *S. capensis* and other African Anabantidae (Cambray and Teugels, 1988). So there are very few data for comparative purposes. Siegfried (1963) reported that Mr. G. Reinhardt observed that 'eggs' (= free embryos) of *S. capensis* hatch after approximately 35 hours at a temperature of 24 °C and that the young are free swimming 4 days after hatching. In the present study the exact time of activation was not established. However, from an early multi-celled blastodermal cap stage to

hatching took 40,5 h at 22–23 °C. During the summer months (November, December and January) Barnard (1943) collected and examined 'juveniles' (= larval fish) of *S. capensis* from 8 mm upwards. Barnard (1943) included drawings of 8 and 10 mm larval *S. capensis*.

Mayekiso (1986) found that the ova of *S. bainsii* are released when their wet diameter is between 0,99 and 1,24 mm. For *S. capensis* the diameter at release is between 1,0 and 1,4 mm.

Since the eggs of *S. capensis* were highly adhesive the oil globule may have acted as a buoyancy organ and possibly had very little of a functional role to play until the embryo hatched and had mobility. The adhesive organ on the dorsum of the head functioned to keep the embryo in one place. If disturbed, the free embryo could move to another site and the possible buoyancy of the oil globule would be of importance at that stage. During the development of *S. capensis* the oil globule migration and its subsequent division would indicate that it was functioning as a temporary swimbladder. The movement and division of the oil globule occurred before swimbladder inflation. Initially the free embyros were positioned with their ventral surfaces upwards. The oil globule migrated (initially posteriorly then dorsally) and then divided. The two oil globules then lay in a position where the swimbladder was forming. At this stage the orientation of the free embryo changed to dorsal surface upwards which was followed by swimbladder inflation.

The development of the posterior prolongations of the swimbladder in *S. capensis* as described here was similar to that described for *Ctenopoma muriei* (Mörike, 1977: Figs 10 and 11). The posterior prolongations extended as far posteriorly as the caudal skeleton (Fig. 10b).

The pigmentation of the early life history stages of *S. capensis* was unlike that of the co-occurring cyprinid minnow species, which characteristically have stellate melanophores (pers. obs.). Another very good character which could be used to separate *S. capensis* eggs and early free embryonic stages from cyprinids was the presence of the oil globule in the Cape kurpers. In addition the small size and adhesive egg envelope were also good characters to separate these eggs. The heavy pigmentation on the yolk-sac and on the developing embryo would also be characters to separate this species from other co-occurring species. Free embryos and larval fish could easily be separated from other co-occurring fish species by the shape of the swimbladder, large eyes and the distinctive caudal fin shape with its transitory dorsal lobe.

BREEDING BEHAVIOUR

Harrison and du Plessis (1947) were the first to describe the breeding behaviour of *S. capensis*. Their observations were made on fish breeding in a reservoir. The darkly coloured males were 'hostile to each other' and chased others from their territory. The nuptial embrace was observed and described as relatively simple and was accompanied by a whirling movement. Harrison and du Plessis (1947) observed one *S. capensis* guarding a small stump of dead wood and roots which had yellowish eggs adhering to them. All the nests were at a depth of 61–76 cm. The authors carefully examined one nest. They did not find any definite construction and observed that the eggs were distributed haphazardly over an area of approximately 0,092 m^2 (1 ft^2). Siegfried (1963) noted that the spawning bed measured approximately 30 cm in diameter, which agrees with the present aquarium study, and that the male defended an area with a radius of about 50 cm from the centre of the spawning bed. Harrison and du Plessis (1947) found eggs adhering to stones, dead twigs, pieces of wood, roots and weeds, which would indicate that they had not been placed. In the present study the same random pattern of egg laying was also observed and most of the eggs were attached to aquarium gravel. The male alone guards the nest (Siegfried, 1963, and the present study). The nest area did not appear to be cleaned in any way

although there was a shallow depression in the aquarium gravel possibly caused during the spawning act. The eggs, however, were not only found in the depression but also outside this area. This is unlike some of the guarding *Ctenopoma*, such as *C. intermedium*, which have bubble nests and place the eggs in the nest (pers. obs.). Using the reproductive guilds as put forward by Balon (1975, 1985), *S. capensis* belongs in the guarder (B) ethological section, the ecological group is that of the substratum choosers (B. 1), and it is a rock or plant tender and therefore in the reproductive guild B. 1.3 (lithophils) or B. 1.4 (phytophils) (Balon, 1985).

Harrison (1952) recorded small (6,4 mm) *S. capensis* from the Berg River in December 1933. In early summer in the Hex River, 'similar' young *Sandelia* were observed (Harrison, 1952). On December 5 1933, Harrison (1952) collected small *S. capensis* (12,7–25,4 mm long (0,5–1,0 in.)) and suggested that they had been spawned from July to September. From this data set Harrison (1952) speculated that *S. capensis*, may spawn in rivers of the western area in the spring after the floods abate whereas the species in seasonal vleis may spawn earlier when the winter rains restore suitable water conditions. In De Hoop Lake, Siegfried (1963) studied the reproductive cycle of *S. capensis*, and noted that the females underwent 'incomplete' spawning (= serial) at repeated intervals over a prolonged period throughout the months of spring and summer, with two spawning peaks, one during mid-spring and one during mid-summer. Siegfried (1963) also suggested that older fish bred earlier in the season than first-year individuals. In the Wit River it has been recorded that *S. capensis* breed throughout the summer months (this study). The aquarium study verified the serial breeding habit of the Cape kurper. *S. bainsii* have been recorded to spawn repeatedly during the summer breeding season (Mayekiso, 1986).

Field observations of a population of *S. capensis* in the Wit River showed that fish were actively breeding during the middle of November 1988 with water temperatures around 20–23 °C. Several small (*c* 15 cm TL) males, in breeding colours, were chasing females in small circles, however, no actual spawning was observed. The darkened males readily chased away any other sexually active males. Diving revealed that the larger males, some as big as 20 cm TL, were occupying territories between tree roots where the river had eroded the bank. The tree roots were examined for eggs, as was the open gravel area of the smaller males, but no eggs were found. The following month young-of-the-year *S. capensis* were collected amongst the submerged roots of *Gunnera perpensa*. These fish were between 7,4–10,8 mm SL.

HABITAT

Sandelia capensis is confined to the South Coastal Drainage Basins in the Cape Province. This species can tolerate a wide variety of both physical and chemical water conditions (Harrison, 1952). In a recent study Scott and Hamman (1988) suggested that in De Hoop Vlei, a southern Cape Coastal Lake, the major limiting factor for the survival of *S. capensis* was salinity. High salinity levels of up to 60 °/oo eliminated *S. capensis* from certain sites in De Hoop Vlei and when salinity levels were lowered recruitment took place from the freshwater springs in the northern half of the vlei (Scott and Hamman, 1988). Hofmeyr (1966) determined that *S. capensis* is fairly tolerant of sodium chloride and has a median tolerance limit of 10 000 minutes in a 15,6 °/oo sodium chloride solution. However, he suggested that *S. capensis* could not tolerate undiluted sea water. No work has been done on the salinity tolerance of the early developmental stages of this species. Since the early life stages have the least mobility their tolerance of salinity needs to be established.

In the Wit River all the larval and juvenile *S. capensis* were collected from under mats of

vegetation. The adults were collected from this habitat but also from more open areas devoid of aquatic vegetation.

Although *S. capensis* does not have a well-developed labyrinthine organ (Liem, 1963; Peters, 1978), as do the species of *Ctenopoma*, it is a fairly hardy species (Harrison, 1952). Cambray (1978) suggested that the reduction in the supra-branchial organ in *S. capensis* was accompanied by an increase in the gill respiratory area. *S. capensis* also lacks the well-developed series of spines on the edge of the gill-cover which allows more tropical forms such as *C. multispinis* to migrate over land when temporary pools dry out. It is therefore suggested that *S. capensis* are not as well adapted to low oxygen conditions as are many of the *Ctenopoma* species. The lack of adaptation to low oxygen levels was also evident in the early life history of the Cape kurper. The *S. capensis* eggs spawned on the substratum would need adequate oxygen to survive. In comparison some of the *Ctenopoma* species have overcome low oxygen substratum areas by using bubble nests to keep their eggs and free embryos at the air/water interface.

CONSERVATION

At several localities known populations of *S. capensis* have been exterminated by the introduced exotic predator, black bass (*Micropterus salmoides* and *M. dolomieui*). Harrison (1952) reported that the once abundant *S. capensis* population in Paarde Vlei was exterminated by largemouth bass. Harrison (1952) also reported the drastic reduction of *S. capensis* in the Berg River by the introduced smallmouth bass. In the larger pools of the Baviaanskloof River, a tributary of the Gamtoos River system, *S. capensis* have been exterminated by black bass, and the only remaining populations of Cape kurpers were found in the shallow upper reaches of this system (pers. obs.). The guarding *S. capensis* males would be very easily preyed upon by a large predator as the Cape kurpers try to defend their nests.

Adult *S. capensis* are known to be lurking predators (Bruton et al., 1982) which feed on aquatic insects, crustaceans (Siegfried, 1963) and small fish. The lurking behaviour was seen in fish as small as 5 mm NL when they fed on rotifers. In the Wit River population cannibalism has been found.

The early life history stages are known to be the most critical stages in the development of a fish. The early stages of the Cape kurper are guarded by the parental male who chases all other fish including the parental female away from the nest area. Later in their development the larval fish require cover. In the Wit River a population of *S. capensis* was seen to increase after the area became part of the Cockscomb Nature Reserve. Goats and cattle were removed from the area. These animals had previously grazed the aquatic vegetation thereby removing the habitat for larval and juvenile Cape kurpers. Man induced changes in the physical and chemical conditions of the body of water, the lack of suitable cover for larval fish, and the introduction of large exotic predaceous fish species are probably the main threats to populations of this species.

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A fourth contribution to the knowledge of the ethology of the genus *Ceramius* Latreille (Hymenoptera: Vespoidea: Masaridae) in southern Africa.

by

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(Albany Museum, Grahamstown)

*(The order of names is alphabetical and joint authorship should be understood. The same applies to previous papers on the ethology of Hymenoptera by the same authors.)

ABSTRACT

Ethological accounts including nest structure and flower visiting records are given for four species of *Ceramius* Latreille, *C. clypeatus* Richards, *C. micheneri* Gess, *C. toriger* Schulthess and *C. braunsi* Turner. In addition, first flower visiting records are given for *C. caffer* Saussure and *C. metanotalis* Richards. Notes are given on usurpation of nests of *C. braunsi* by *Megachile (Eutricharaea) aliceae* Cockerell (Megachilidae) and the association with this bee of the parasitic bee *Coelioxys (Coelioxys) recusata* Schulz (Megachilidae).

In the discussion the ethological data are used to clarify the species grouping within the genus *Ceramius*.

INTRODUCTION

The present paper is the fourth in a series of publications (Gess and Gess, 1980, 1986 and 1988a) dealing with the ethology of southern African species of the genus *Ceramius* Latreille (Hymenoptera: Masaridae).

The genus *Ceramius* is represented in southern Africa by 19 species belonging to six of the eight species groups suggested by Richards (1962) and revised by Gess and Gess (1986 and 1988a).

It would seem to be desirable to have made ethological studies of all the species and then to have presented these as a study of the ethology of the southern African species as a whole. However, due to lack of certainty associated with finding many of the species, let alone their nests, it has been the authors' policy to publish ethological information as it becomes available and there by to gradually piece together an understanding of the genus and the species groupings within the genus.

In the previous papers accounts were given of the nests of nine species belonging to five groups—Group 2a: *C. cerceriformis* Saussure; Group 3: *C. nigripennis* Saussure and *C. jacoti*

Richards; Group 5: *C. lichtensteinii* (Klug); Group 6: *C. rex* Saussure; Group 8: *C. bicolor* (Thunberg), *C. linearis* Klug, *C. capicola* Brauns and *C. socius* Turner. In the present paper accounts are given for a further four species—Group 2b: *C. clypeatus* Richards; Group uncertain: *C. micheneri* Gess; Group 3: *C. toriger* Schulthess and *C. braunsi* Turner.

As *Ceramius* provisions its young with pollen and nectar flower visiting records are of importance. Gess and Gess (1989) presented flower visiting records for 14 species. In the present paper records are given for a further two species, *C. caffer* Saussure and *C. metanotalis* Richards and additional records are given for some species for which previous records were extremely scant.

The paper is structured on the species groupings and the data presented are used to discuss the characterization of the species groups.

ETHOLOGICAL ACCOUNTS

Group 2b

Group 2b is constituted of *Ceramius clypeatus* Richards and *C. richardsi* Gess.

Geographic distribution

Both species appear to be restricted to the area lying between the Olifants River Mountains in the south and Namaqualand in the north.

Ethology

An account of flower visiting by *C. clypeatus* in the Clanwilliam District was presented by Gess and Gess (1988a and 1989). Further observations on flower visiting and an investigation of nesting were made in the Clanwilliam District during the period 16–20.x.1989.

Nothing is known of the nesting or flower visiting behaviour of *C. richardsi*.

Description of nesting area

Two nesting areas of *C. clypeatus* were located in the Clanwilliam district, a brief account of the soils and vegetation of which was given in Gess and Gess (1988a). Both areas are situated above and to the east of the Clanwilliam Dam.

One is a levelled sparsely vegetated stoney area in the grounds of the Clanwilliam Dam resort. The soil is compacted sand with sufficient clay to make it malleable when mixed with water. At the time of the study water was available from a roadside trickle. Most of the nests were partially concealed either amongst stones or under bushes. The nests were aggregated in small groups, for example five nests were grouped within a radius of 15 cm.

The other area is a sparsely vegetated slope above the old Olifants River Valley Road above Caleta Cove (32°14′20″S, 18°55′45″E), on the east bank of the Clanwilliam Dam (Fig. 1). The soil is extremely hard compacted sand with sufficient clay to make it malleable when mixed with water. Water was available from a roadside pool (Fig. 7). The nests were not concealed nor grouped but occurred singly in bare areas between bushes.

Plants visited

Gess and Gess (1988a and 1989) established that *C. clypeatus* is a common visitor to the flowers of *Aspalathus spinescens* Thunb. subsp. *lepida* (E. Mey) Dahlgren (Leguminosae: Papilionatae) in the Clanwilliam district.

Fig. 1. Old Olifants River Valley Road to the east of the Clanwilliam Dam; nesting area of *Ceramius clypeatus* Richards, *C. micheneri* Gess and *C. braunsi* Turner in vicinity of bare patch in middle distance, above Caleta Cove.

Further investigation in October 1989 confirmed this association and in addition revealed that *C. clypeatus* is also a common visitor to flowers of *Aspalathus linearis* (Burm. *f.*) Dahlgren (Rooibos Tea). A sample (5 ♀♀, F. W. and S. K. Gess, 16.x.1989) was taken in the grounds of the Rooibos Co-op, Clanwilliam. Above Caleta Cove *C. clypeatus* was found to be visiting a third species of *Aspalathus*, *A. pulicifolia* Dahlgren. *A. pulicifolia* was growing in an area of hard compacted sandy soil not favoured by *A. spinescens* or *A. linearis* which seem to favour looser sandy soil. A sample was taken (2 ♀♀ and 2 ♂♂, F. W. and S. K. Gess; 1 ♀, D. W. Gess; all 19.x.1989).

It is of note that all three forage plants are *Aspalathus* species. All other plants in flower were sampled for insect visitors. None was found to be visited by this wasp.

The posture of *C. clypeatus* on all three species of *Aspalathus* is constant and is as described by Gess and Gess (1989: 103 and figs 5, 6 and 7) for this wasp on *A. spinescens* subsp. *lepida*. That is briefly, the wasp, when alighting on one of the small pea flowers, grasps the alae with the second and third pairs of legs and curves the abdomen down beneath the flower aiding its balance whilst it imbibes nectar from the base of the standard or consumes pollen directly from the anthers.

Provision

The cell provision of *C. clypeatus* is of the typical *Ceramius* type being a firm relatively dry nectar and pollen loaf (Fig. 2).

Samples of pollen were taken from the crop of a female and from the provision from four cells from the nests of four further females from the Clanwilliam Dam resort and from the provision from one cell from a nest from Caleta Cove. In each sample the pollen was found to be all of one kind. Pollen from all the samples was of the "Aspalathus type" (triangular sided and with each side 25 μ) matching that of *Aspalathus spinescens* subsp. *lepida* from the Clanwilliam Dam and that of *Aspalathus pulicifolia* from Caleta Cove.

Water collection

Females of *C. clypeatus* were observed collecting water from a roadside trickle at the Clanwilliam Dam resort and from a small pool above Caleta Cove. In all cases water was being imbibed on the wet soil at the edge of the water source. No females were seen to alight on the water surface.

Male behaviour

Male *C. clypeatus* were not seen at water or in the nesting areas. They were, however, observed visiting flowers co-incident in time with the females and several instances of a male mounting a female were observed.

Description of the nest

The nest consists of a multi-cellular subterranean burrow surmounted by a curved tubular mud turret (Figs 3 and 4a). The turret is constructed of mud pellets roughly smoothed on the outside and well smoothed on the inside. Some interstices are left open distally. The turret and shaft opening are of equal diameters. The main shaft descends sub-vertically and for the greater part of its length is of the same diameter as the entrance. Near the lower end of the shaft there is a short wider section forming a "bulb" below which the shaft continues with a diameter equalling that of the upper section of the shaft. The main shaft at its base curves outwards to form a short lateral shaft terminating in a cell which lies sub-horizontally. Within an excavated-cell there is a constructed mud-cell sealed at the neck with a mud-plug. The section

Fig. 2. Provision, firm nectar and pollen loaf, from a cell of *Ceramius clypeatus* Richards (×3).

Fig. 3. Mud turret surmounting burrow of *Ceramius clypeatus* Richards (×1,5).

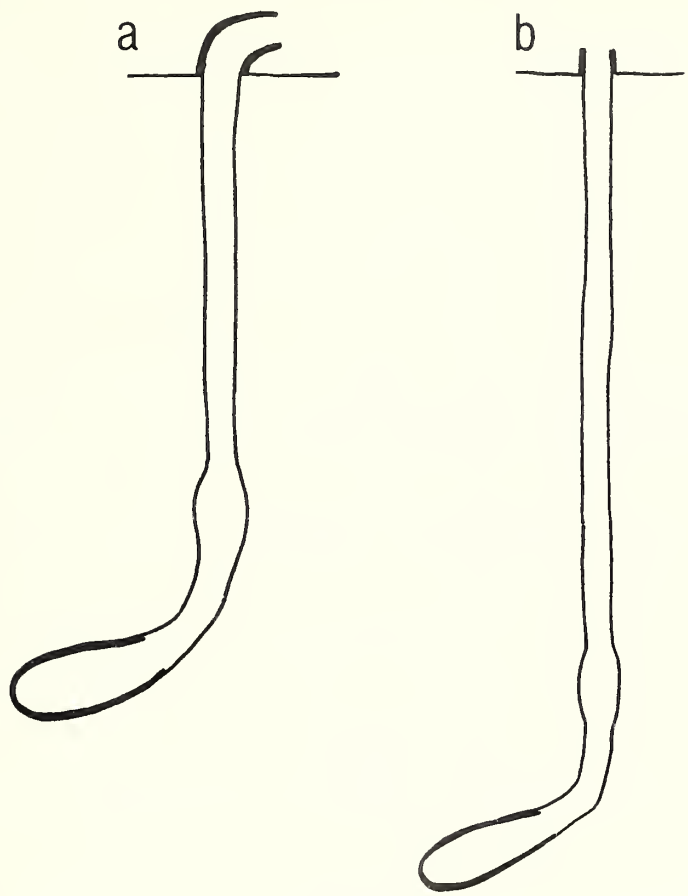

Fig. 4. Vertical plans of turrets and underground workings of nests of *Ceramius clypeatus* Richards (a) and *C. micheneri* Gess (b) (× 1).

of the secondary shaft between the cell and the main shaft is filled with soil and is sealed off from the main shaft. Successive cells lie to one side of the shaft in a group.

Method of construction of the nest, oviposition and provisioning

Water is required for nest construction. The turret is constructed at an early stage in shaft sinking. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same inner diameter as the shaft. The walls of the turret are approximately 1 mm thick. Pellets are added to the turret in such a way that it soon curves over. After turret construction is completed further pellets extracted in shaft sinking are discarded at some distance from the nest.

After the construction of the first cell is completed oviposition takes place and is followed by provisioning. The provision, a mixture of pollen and nectar, is in the form of a relatively dry firm loaf which only partially fills the cell.

The completed provisioned cell is sealed with a mud-plug constructed just within the mouth of the cell and having its outer face concave. The sub-horizontal shaft is then firmly packed with soil until the sub-vertical shaft is reached, when it is sealed off with a mud plate.

Further cells terminate secondary shafts and are prepared in a similar fashion to the first.

A sample of twelve nests was investigated. All were new nests, that is in no instance had a wasp reused her maternal nest. Seven nests were single-celled, one was four-celled and the remaining four were nests which had not yet reached the stage of cell excavation. Nest measurements are given in Table 1.

Table 1.

Measurements of nests of *Ceramius clypeatus* Richards.

	Range (mm)	Average (mm)	Sample size
Height of turret	9–13	10,8	9
Diameter of shaft	4,5–4,5	4,5	9
Diameter of bulb	7–9,5	8,3	6
Diameter of excavated-cell	8–9	8,5	4
Length of shaft above bulb	42–68	56,3	6
Length of bulb	10–15	12,5	6
Total length of vertical shaft	67–85	78,3	6
Length of excavated-cell	20–21 (approximate)		

Group: uncertain

Placement of *Ceramius micheneri* Gess into any particular species group is uncertain. The affinities of the species, judged purely from consideration of morphological characters, were stated by Gess (1968) to be with the species of the *Ceramioides* group of species (*C. cerceriformis* Saussure, *C. peringueyi* Brauns, *C. clypeatus* Richards and *C. richardsi* Gess) and possibly with the group of four species comprising *C. nigripennis* Saussure, *C. toriger* Schulthess, *C. braunsi* Turner and *C. jacoti* Richards—that is, with groups 2 and 3 of Richards (1962) and Gess and Gess (1986 and 1988a). For some reason, at present no longer clear, Gess and Gess (1986 and 1988a) tentatively assigned *C. micheneri* to Group 3 rather than Group 2. On ethological grounds this assignation is now recognised as having been incorrect (see Discussion).

Geographic distribution

C. micheneri is known only from the Olifants River Valley between Citrusdal and Klawer. It has been recorded previously from Citrusdal and from Olifants River between Clanwilliam and Klawer (Gess, 1968 and 1973).

The present observations were made in the Clanwilliam District above Caleta Cove (Fig. 1) during the period 16–20.x.1989.

Ethology

Nothing was previously known of the flower visiting and nesting behaviour of *C. micheneri*. The present account indicates in both flower association and nest structure affinities with Group 2b.

Description of nesting area

Three nests were located on a sparsely vegetated slope above the old Olifants River Valley Road above Caleta Cove (Fig. 1). The soil is extremely hard compacted sand with sufficient clay to make it malleable when mixed with water. Water was available from a roadside pool (Fig. 7). The nests were not concealed nor grouped but occurred singly in bare areas between bushes.

Plants visited

C. micheneri has not previously been recorded visiting flowers. It is here recorded as visiting the small yellow pea flowers of *Aspalathus pulicifolia* (Leguminosae: Papilionatae) at Caleta Cove. A sample was taken (2♀♀ and 4♂♂, F. W. Gess and S. K. Gess, and 2♀♀, D. W. Gess, all 19–20.x.1989).

All other plants in flower were sampled for insect visitors. None was found to be visited by this wasp.

Provision

Provision from a nest of *C. micheneri* investigated at Caleta Cove was examined. It was in the form of a relatively dry nectar and pollen loaf. The pollen was found to be all of one kind and to match that of *A. pulicifolia*.

Water collection

Females and males of *C. micheneri* were observed on wet soil at the edge of a pool at Caleta Cove. None was seen to alight on the water surface.

Male behaviour

Male *C. micheneri* were observed in company with females at water and visiting the forage plant, however, no instances of pairing were observed. A male was found together with a female in her nest.

Description of the nest

The three nests investigated all consisted of a subterranean burrow surmounted by a low vertical cylindrical mud turret (Fig. 4b) constructed from mud pellets cemented together and smoothed on the inside. The inner diameter equalled that of the descending sub-vertical main shaft.

One nest was in an early stage of construction and lacked a cell. In the other two nests the main shaft at its base curved outwards to terminate in an ovoid cell lying sub-horizontally. At some little distance above the base of the vertical shaft it was widened to form a "bulb".

Within each excavated-cell had been constructed a mud-cell with walls of somewhat less than 1 mm in thickness and smoothed on the inside.

Nest measurements are given in Table 2.

Table 2.

Measurements of nests of *Ceramius micheneri* Gess.

	Range (mm)	Average (mm)	Sample size
Height of turret	3–4	3,7	3
Diameter of shaft	3,5–4,0	3,7	3
Diameter of bulb	5–6	5,5	2
Diameter of excavated-cell	5–6	5,5	2
Length of shaft above bulb	75–85	80,0	2
Length of bulb	12–12	12,0	2
Total length of vertical shaft	95–100	97,5	2
Length of excavated-cell	16–17	16,5	2

Group 3

Group 3 is constituted of four species, *Ceramius braunsi* Turner, *C. jacoti* Richards, *C. nigripennis* Saussure and *C. toriger* Schulthess.

Geographic distribution

Group 3 as a whole has a relatively wide distribution in the western and southern Cape, however, the distribution of each of the four species is distinct.

C. braunsi has been recorded from Vanrhynsdorp lying below and to the west of the Bokkeveldberge, from the Olifants River Valley and the western foothills of the Cederberg, south of the Tankwa Karoo and the Hex River Mountains at Worcester and in the east from the southern Great Karoo at Willowmore (Richards, 1962; Gess, 1965, 1968 and 1973; Gess and Gess, 1988a and present paper).

C. jacoti Richards is also a southern species but appears to be more restricted in distribution than *C. braunsi*, all records being from east of Worcester, that is from Hex River in the west to Oudtshoorn in the Little Karoo in the east (Richards, 1962; Gess, 1965; Gess and Gess 1988a and present paper).

C. nigripennis seems to be a Namaqualand species being particularly characteristic of the Namaqualand Klipkoppe. It has been recorded from the Swart Doringrivier north to Nababeep, from the Hester Malan Nature Reserve, 12 km east of Springbok in the Carolusburg and from the mountainous area to the west and southwest of Springbok (Richards, 1962; Gess, 1965 and 1968; Gess and Gess, 1986 and 1988a; present paper).

C. toriger has been recorded from the escarpment formed by the Bokkeveldberge to the east of the Knersvlakte, the Skuinshoogte Pass, 15 km north of Nieuwoudtville on the road to Loeriesfontein, eastwards to Calvinia, and southwards through the Tankwa Karoo lying to the east of the Cederberg to Karoopoort, 43 km ENE of Ceres on the road to Sutherland (Richards, 1962; Gess 1965 and 1968; present paper).

Ethology

Accounts of flower visiting by *C. braunsi*, *C. jacoti* and *C. nigripennis* were given by Gess and Gess (1988a and 1989; 1988a and 1989; and 1986 and 1989, respectively). A flower visiting record for three male *C. toriger* was given in Gess (1968). Further flower visiting records for *C. braunsi*, *C. nigripennis* and *C. toriger* are given in the present paper.

Accounts of nesting by *C. jacoti* and *C. nigripennis* were given by Gess and Gess (1986). Accounts of nesting by *C. braunsi* and *C. toriger* are given in the present paper.

Plants visited

The only flower visiting records for *C. toriger* previously available were for three males "on blue-rayed Compositae" (Gess, 1968) indicating a possible association with Compositae.

This association is supported by the observation of both males and females visiting the flowers of *Pteronia* cf. *divaricata* (Berg.) Less. and *Berkheya fruticosa* (L.) Ehrh. (both Compositae) in the Skuinshoogte Pass, 3–8.x.1989. Samples were taken (visiting the yellow flowers of *P. divaricata*, 2 ♀♀ and 5 ♂♂, D. W. Gess; visiting the yellow flowers of *B. fruticosa*, 2 ♀♀, D. W. Gess, and 1 ♀ and 2 ♂♂, F. W. Gess and S. K. Gess). In addition one female was collected foraging on *Athanasia trifurcata* (L.) L. in Karoopoort, 3.xii.1989 (S. K. Gess).

All other plants in flower were sampled for insect visitors. None was found to be visited by this wasp.

Gess and Gess (1989: 102–103 and figs 3 and 4) recorded *C. braunsi* as visiting primarily Compositae, *Athanasia trifurcata* (L.) L., *Arctotis laevis* Thunb. and *Pentzia* sp. and occasionally *Aspalathus spinescens* subsp. *lepida* (Leguminosae: Papilionatae). Pollen gathering on the capitula of *Arctotis laevis* was described. Visits to *A. spinescens* appeared to be for nectar only.

During the present study *C. braunsi* was again found commonly on the capitula of *Athanasia trifurcata* and *Arctotis laevis* to which it was by far the most common visitor. Samples were taken (*Athanasia trifurcata*, 45 ♀♀ and 1 ♂, F. W. Gess and S. K. Gess, and 4 ♀♀, D. W. Gess, all Caleta Cove and *Arctotis laevis*, 2 ♀♀, F. W. Gess and S. K. Gess, and 2 ♀♀, D. W. Gess, all Clanwilliam Dam resort). Although the insects visiting *Aspalathus* species were sampled no visits by *C. braunsi* were observed. All other plants in flower were sampled for insect visitors. None was found to be visited by this wasp.

Plant visiting records for *C. nigripennis* are all for members of the family Compositae: *Dimorphotheca sinuata* DC., *Pentzia suffruticosa* (L.) Hutch. ex Merxm., *Berkheya fruticosa* (L.) Ehrh. and *Hirpicium alienatus* (Thunb.) Druce (Gess and Gess, 1988a and 1989).

The fidelity of this species to Compositae is supported by new flower visiting records resulting from further plant sampling.

Hester Malan Nature Reserve, Springbok, 10–11.x.1989:

Pentzia suffruticosa (L.) Hutch. ex Merxm. 1 ♀, F. W. and S. K. Gess; 1 ♀, D. W. Gess
Berkheya fruticosa (L.) Ehrh. 3 ♀♀, 1 ♂, F. W. and S. K. Gess; 1 ♂, D. W. Gess
Hirpicium sp. 2 ♀♀, F. W. and S. K. Gess; 2 ♂♂, D. W. Gess
Arctotheca calendula (L.) Levyns 1 ♂, D. W. Gess

Nababeep, 12–13.x.1989:

Berkheya fruticosa (L.) Ehrh. 3 ♀♀, 1 ♂, F. W. and S. K. Gess; 1 ♂, D. W. Gess

Ceramius toriger Schulthess and *Ceramius braunsi* Turner

The present observations concerning *C. toriger* were made in the Skuinshoogte Pass, 15 km north of Nieuwoudtville on the road to Loeriesfontein and between Nieuwoudtville and Calvinia during the period 3–8.x.1989, and in Karoopoort, 43 km ENE of Ceres on the road to Sutherland on 3.xii.1989.

Those concerning *C. braunsi* were made in the Clanwilliam District, at the Clanwilliam Dam, at the resort and at Caleta Cove, and at Zeekoevlei, *c* 20 km west of Clanwilliam on the road to Graafwater during the period 16–20.x.1989.

Descriptions of nesting areas

A nesting area of *C. toriger* was located in the Skuinshoogte Pass. The vegetation is probably closest to Acocks Veld Type 28, Western Mountain Karoo (Acocks, 1953 and 1957). The nests were situated on a steep slope 50 m from a small farm dam (Fig. 5). The slope was mostly eroded down to the underlying shale, soil remaining around the bases of old woody shrubs and as derelict termite heaps. It was these islands of soil which had been used by the wasps as nesting sites (Fig. 6). The nests were either solitary or in groups, the largest group being of five nests in an area 50 cm in diameter.

A nesting area of *C. braunsi* was located on a sparsely vegetated slope above the old Olifants River Valley Road above Caleta Cove (Figs 1 and 7). The vegetation of this area is categorized by Moll *et al* (1984) as a "Mosaic of Dry Mountain Fynbos and Karroid Shrublands". The soil is extremely hard compacted sand with sufficient clay to make it malleable when mixed with water. Water was available from a roadside pool. The nests were grouped in aggregations of 20 or more. Sloping ground was favoured (Fig. 8). Water erosion indicated that the aggregations had existed at the same sites over a considerable number of years.

Provision

The provision of both species is of the typical *Ceramius* type being a firm relatively dry pollen loaf.

Provision from four nests of *C. toriger* investigated in the Skuinshoogte Pass was examined. The pollen was found to be all of one kind and to match that of *Berkheya fruticosa*.

The pollen from samples taken from the provision and from crop contents of *C. braunsi* was all of the spiny composite type.

Water collection

The females of all four species in Group 3 alight on the water surface when imbibing water.

Large numbers of both males and females of *C. toriger* were observed at water at two small farm dams and at puddles in a stream bed in the Skuinshoogte Pass and at two small farm dams between Nieuwoudtville and Calvinia. The females alighted on the surface of the water and never at the edge on the mud. Activity at water lasted from mid-morning to mid-afternoon.

Gess and Gess (1988a) recorded females of *C. braunsi* as having been collected on very wet sand, that is supersaturated sand covered with a film of water, at the edge of a dam.

During the present study both females and males were observed on the water surface of the pool at Caleta Cove.

Fig. 5. Skuinshoogte, 15 km north of Nieuwoudtville on the road to Loeriesfontein; nesting area of *Ceramius toriger* Schulthess.

Fig. 6. Island of soil; a nesting site of *Ceramius toriger* Schulthess; mud turret surmounting a nesting burrow in foreground.

Male behaviour

Male *C. toriger* were observed in company with females visiting the forage plant and at water. The males "waited" in large numbers on the ground at some distance from the water being visited by females, however, no instances of pairing were observed.

Ten nests of *C. toriger* were investigated, all in the late afternoon in damp weather when the builders were sheltering in their nests. A male was found in company with a female in two of these nests.

Male *C. braunsi* were observed in company with females at water and visiting flowers, however, no instances of pairing were observed. No males were observed in association with nests.

Description of the nests

The nests of *C. toriger* and *C. braunsi* consist of a subterranean burrow surmounted by a curved tubular mud turret (Figs 9, 10 and 11). The turret is constructed of mud pellets cemented together and well smoothed on the inside so that few interstices remain. The main shaft of the burrow is short and vase-shaped, having the upper part of the same diameter as that of the turret and the lower part, the "bulb", of a diameter up to two and a half times greater depending upon the number of cells present. From the "bulb" extend one or more very short sub-vertical secondary shafts each terminating in an excavated cell within which is a constructed mud-cell the neck of which extends into the secondary shaft. All completed cells are sealed and the secondary shaft between the sealed cell and the main shaft is filled with tightly packed earth and its opening to the main shaft is sealed with a mud plate.

Method of construction of nest, oviposition and provisioning

At the commencement of nesting a female may either initiate a new nest or enlarge the nest from which she emerged.

Water is required for nest construction. At an early stage in nesting both nest initiators and nest enlargers construct a turret surmounting the main shaft. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same inner diameter as the shaft.

After turret construction has been completed further mud pellets extracted in shaft sinking are discarded in close proximity to the nest.

The first mud cell having been carefully smoothed on the inside oviposition takes place and is followed by provisioning.

No egg was obtained for *C. toriger*. That of *C. braunsi* was as is usual for *Ceramius* laid loose in the bottom of the empty cell. The single egg obtained was curved, yellow, 6 mm from tip to tip across the bow and 1,5 mm in diameter. The provision is in the form of a relatively dry firm nectar and pollen loaf which partially fills the cell.

The completed provisioned cell is sealed, the shaft is firmly packed with soil until the "bulb" is reached and the opening is then sealed off with a mud plate.

Further cells are prepared in a similar fashion to the first.

Samples of 10 *C. toriger* and eight *C. braunsi* nests were investigated.

Fig. 7. Area above Caleta Cove, Clanwilliam Dam; bare slope, nesting site of *Ceramius braunsi* Turner; roadside pool, water source for *C. clypeatus* Richards, *C. micheneri* Gess and *C. braunsi*.

Fig. 8. Part of an aggregation of nests of *C. braunsi* Turner.

Fig. 9. Mud turret surmounting burrow of *Ceramius toriger* Schulthess (×1,5).

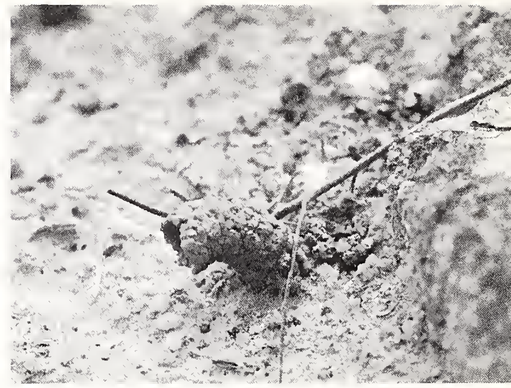

Fig. 10. Mud turret surmounting burrow of *Ceramius braunsi* Turner (×1,5).

Of the *C. toriger* nests three were new nests which were surmounted by turrets but which had not yet reached the level of the bulb, and seven were old reused nests surmounted by newly constructed turrets (Table 3). Nest measurements are given in Table 5.

TABLE 3.

Details pertaining to 10 nests of *Ceramius toriger* Schulthess investigated in the Skuinshoogte Pass, 15 km north of Nieuwoudtville on the road to Loeriesfontein.

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cell contents	Remarks
1	New	Present	0	—	♀ *C. t.*
2	Old, reused	Present	5	A B/C B/C E F	♀ *C. t.*
3	Old, reused	Present	7	A A A A A I X	—
4	Old, reused	Present	3	A A I	—
5	Old, reused	Present	4	A B/C B/C I	♀ *C. t.*
6	Old, reused	Present	5	A B/C B/C E F	♀&♂ *C. t.*
7	Old, reused	Present	4	A A B/C F	♀ *C. t.*
8	Old, reused	Present	6	A A A B/C B/C F	♀&♂ *C. t.*
9	New	Present	0	—	—
10	New	Present	0	—	—

Key: A. Cell open containing old cocoon from which adult wasp has emerged.
B. Cell closed, containing pupa in cocoon.
C. Cell closed, containing pre-pupa in cocoon.
E. Cell closed, containing mature larva prior to cocoon spinning.
F. Cell either open or closed, containing still feeding immature larva.
I. Cell open, empty.
X. Cell either open or closed, development of young aborted.
C. t. = *Ceramius toriger* Schulthess

All eight nests of *C. braunsi* were surmounted by turrets, seven nests were newly excavated and one was an old reused nest (Table 4). Of particular note was the reuse of a cell containing a cocoon from which a wasp had emerged. Such reuse of an old cell had not previously been recorded for Group 3. Nest measurements are given in Table 5.

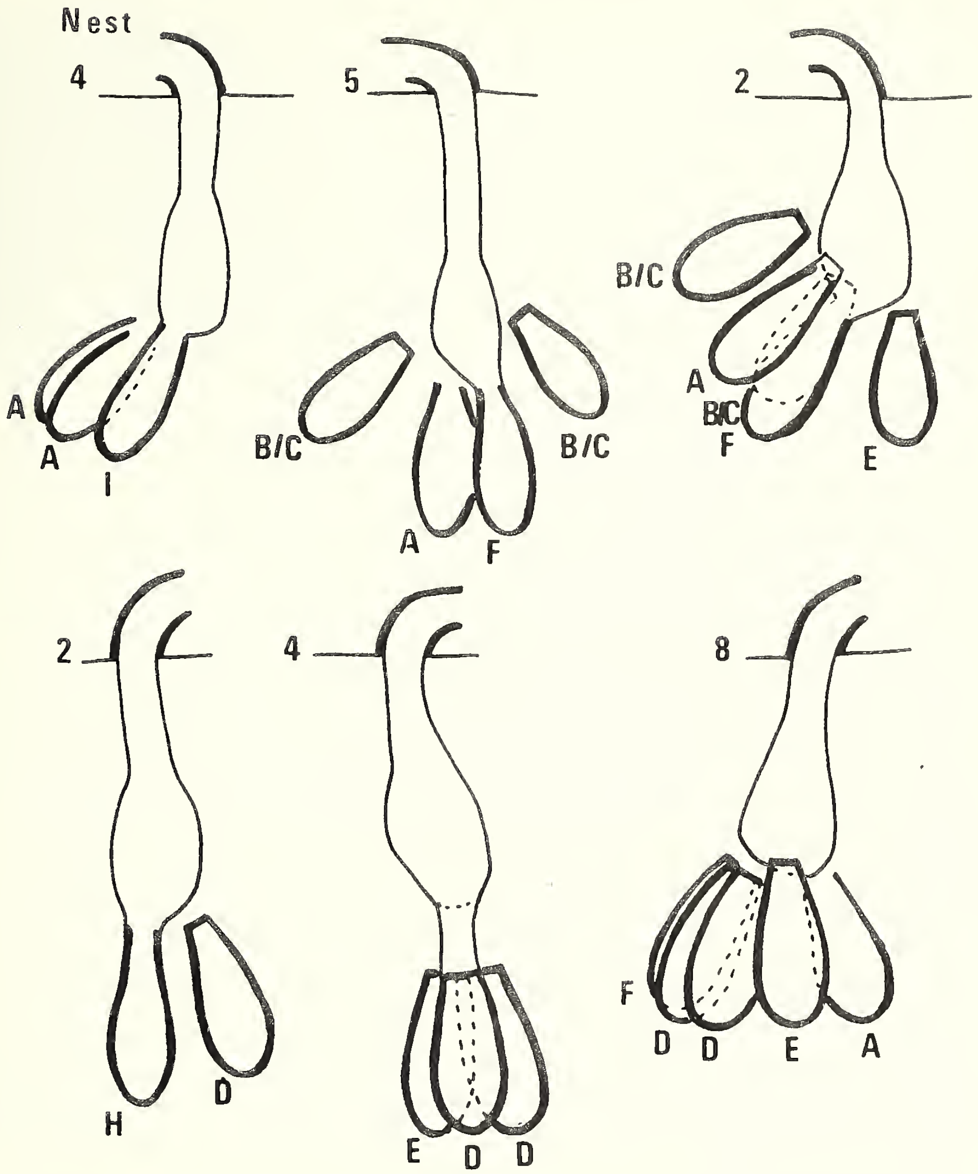

Fig. 11. Vertical plans of turrets and underground workings of three nests of *Ceramius toriger* Schulthess (above) and of three nests of *C. braunsi* Turner (below) (× 1). For key to lettering see tables 3 and 4.

TABLE 4

Details pertaining to 8 nests of *Ceramius braunsi* Turner investigated above Caleta Cove, Clanwilliam.

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cell contents	Remarks
1	New	Present	1	I	♀ *C. b.*
2	New	Present	2	H D	♀ *C. b.*
3	New	Present	1	I	♀ *C. b.*
4	New	Present	3	E D D	♀ *C. b.*
5	New	Present	1	Z	*M. (E.) a.* seal in shaft
6	New	Present	1	Z	*M. (E.) a.* ♀ in nest
7	New	Present	1	Z	*M. (E.) a.* seal in shaft
8	Old, reused	Present	5	A E D D F	—

Key: A. Cell open containing old cocoon from which adult wasp has emerged.
D. Cell closed, containing mature larva spinning cocoon.
E. Cell closed, containing mature larva prior to cocoon spinning.
F. Cell either open or closed, containing still feeding immature larva.
H. Cell open, containing egg without provision.
I. Cell open, empty.
Z. New cell containing bee cell.
C. b. = *Ceramius braunsi* Turner
M. (E.) a. = *Megachile (Eutricharaea) aliceae* Cockerell

TABLE 5.

Measurements of nests of *Ceramius toriger* Schulthess and *Ceramius braunsi* Turner.

	Range (mm)		Average (mm)		Sample size	
	C. t.	*C. b.*	*C. t.*	*C. b.*	*C. t.*	*C. b.*
Height of turret	7–10	9–11	8,0	10,3	9	7
Diameter of shaft	4–5	4–5	4,6	4,5	9	8
Diameter of bulb	15–22	16–23	17,3	19,3	6	8
Diameter of excavated-cell	9–9	10–11	9	10,3	5	5
Length of shaft above bulb	7–20	11–59	13,2	23,7	6	8
Length of bulb	15–22	16–23	17,3	19,4	6	8
Total length of main shaft	26–36	30–78	30,5	43,3	6	8
Length of excavated-cell	18–19	18,5–20	18,2	19,5	5	5

Associated insects

The leaf cutting bee *Megachile (Eutricharaea) aliceae* Cockerell (Megachilidae) and the nest parasite *Coelioxys (Coelioxys) recusata* Schulz (Megachilidae) were observed in attendance on nests of *C. braunsi*. A sample was taken; male and female *M. (E.) aliceae* and female *C. recusata* were found to be present.

Three of the eight nests of *C. braunsi* investigated were found each to contain a petal-cell (Fig. 12). A further nest thought to be that of *C. braunsi* also contained a petal-cell. All of the nests were new and one-celled. Two of the nests were closed with a final bee seal but in each of the other two, in which the petal-cells were still being constructed, a female *M. (E.) aliceae* was found in the nest.

Fig. 12. Petal cell of *Megachile (Eutricharaea) aliceae* Cockerell (Megachilidae) constructed in a cell of *Ceramius braunsi* Turner. (×1,5).

The bee's flask-shaped petal-cells had been constructed within the wasp's cells in such a way that the bee's cells entirely filled the wasp's cells. Three of the petal cells were constructed from pink petals and the fourth from yellow petals. The pink petals matched those of a pink flowered *Pelargonium* species growing close by, which was found to have petals cut off and which was observed to be visited by *M. (E.) aliceae*. The yellow "petals" appeared to be cut from composite ray florets.

The provision was syrupy in nature and contained mixed pollen of three types. The pollen was compared with that of the plants in flower in the nesting area. One of the pollens matched that of a yellow flowered *Homeria* sp. (Iridaceae), another was of the spiny composite type and the third, small and thin walled, was possibly "mesem".

In the two nests in which a final bee seal had been constructed, the sealed petal-cell had been surmounted by a mud-seal, the shaft above the cell had been filled with earth and a final seal had been constructed across the shaft entrance beneath the mud turret. The final seal had been constructed from a layer of petals covered with a layer of mud.

M. (E.) aliceae cells have previously been recorded from burrows of *Parachilus insignis* (Saussure) (Eumenidae) at Hilton, Eastern Cape Province (Gess and Gess, 1976), *Paravespa (G.) mima* Giordani Soika (Eumenidae) at Tierberg, Prince Albert, southern Cape Province (Gess and Gess, 1988b) and *C. nigripennis* at Mesklip, 20 km south of Springbok, Namaqualand (Gess and Gess, 1986). In all instances the bee's cells were orientated vertically.

The presence of *C. (C.) recusata* Schulz is of interest as *Coelioxys* is known to be a parasite in nests of *Megachile.*

Group 6

Group 6 is constituted of three species, *Ceramius caffer* Saussure, *C. metanotalis* Richards and *C. rex* Saussure.

Geographic distribution

The distributions of *C. caffer*, *C. metanotalis* and *C. rex* are poorly known, however, available collecting records indicate very distinct and restricted distributions within the Western Cape: *C. caffer* to the south of the Olifants River Mountains; *C. metanotalis* north of these mountains but south of Namaqualand; and *C. rex* in the area of Namaqualand termed Klipkoppe.

C. caffer was described from "Cape of Good Hope" (Saussure, 1855). It is recorded from Stellenbosch, 1888 (1 ♂ in Richards, 1962 and a further 3 ♂♂ and 2 ♀♀ in Gess, 1965) and 1908 (5 ♀♀ in Richards, 1962 and a further 26 ♀♀ in Gess, 1965). Two further records (Albany Museum Collection) are presented in the present paper: Tulbagh, xi.1947, 1♀, J. G. Theron and 8 km ENE of Ceres at the western end of the Theronsberg Pass, 29.xi.1989, 1 ♀, F. W. Gess and S. K. Gess.

C. metanotalis was originally described from Calvinia, Nieuwoudtville and "Capland" (Richards, 1962); additional material from Bulshoek, Klawer-Clanwilliam was noted by Gess (1965). Additional records are here presented. These are from 30 km north of Clanwilliam on the N7 road to Klawer above the Bulshoek Dam, 17.x.1989: 2 ♀♀, F. W. and S. K. Gess; 3 ♂♂, D. W. Gess.

An account was given in Gess and Gess (1988a) of the search for *C. rex* which until it was found nesting, not uncommonly, in the Hester Malan Nature Reserve in October 1987 had been known only from three specimens: the type specimen, a female labelled Cape Colony, which was described by de Saussure in 1855; a female collected at Garies in Namaqualand in 1931 (S. A. M. Staff); and a male collected at Garies in 1970 (Dr and Mrs H. Townes). Due to the limited knowledge of this species it seems useful to record additional collecting records. These records represent samples not sightings which were more numerous. All are for the area known as Namaqualand Klipkoppe.

Hester Malan Nature Reserve, Springbok, 10–11.x.1989: 2♀♀, F. W. and S. K. Gess.

W end of Wildeperdehoek Pass, 29° 56′ 21″S, 17° 37′ 30″E, 14.x.1989: 2 ♀♀, F. W. Gess and S. K. Gess; 1 ♀, D. W. Gess.

Nababeep, 12–13.x.1989: 1 ♂, D. W. Gess.

Ethology

An account of flower visiting, water collection and nesting by *C. rex* was given by Gess and Gess (1988a). A further record of flower visiting for *C. rex* and first records for *C. capensis* and *C. metanotalis* of are presented in the present paper.

Flower visiting

Flower visiting records are few, however, they all support an association between *Ceramius* Group 6 and Compositae.

Gess and Gess (1988a and 1989) recorded a female *C. rex* visiting *Berkheya spinosissima* (Thunb.) Willd and supported this record with analyses of nest provision and crop contents. In the present paper one record of a male visiting flowers of *Pteronia* sp. A (Compositae) is presented (Nababeep, 12–13.x.1989, D. W. Gess).

Only one record of flower visiting by *C. caffer* has been obtained. This is for a female visiting flowers of *Berkheya carlinifolia* (DC.) (Compositae) (18 km ENE of Ceres at the western end of the Theronsberg Pass, 29.xi.1989, F. W. and S. K. Gess).

C. metanotalis is recorded foraging on *Athanasia trifurcata* (L.) L. (30 km N of Clanwilliam on the N7 road to Klawer above the Bulshoek Dam, 17.x.1989, 2 ♀♀, F. W. & S. K. Gess and 2 ♂♂, D. W. Gess).

All other plants in flower in the areas where these wasps were collected were sampled for insect visitors. No others were found to be visited by these wasps.

Water collection

Water collection by *C. rex* was observed in the Hester Malan Nature Reserve, Springbok, by Gess and Gess (1988a). The wasps collected water from small pools in a river bed. This behaviour has been confirmed by further observations in the Hester Malan Reserve and also at the western end of the Wildeperdehoek Pass to the south west of Springbok.

One male *C. metanotalis* was collected at a small earthen dam above the Bulshoek Dam in close proximity to the forage plants indicating that this was probably the water source for females nesting in the area.

DISCUSSION

Gess and Gess (1986 and 1988a) proposed the use of ethological characters in conjunction with morphological characters in defining species groups in *Ceramius*. Attention was drawn to the considerable constancy of nest plan exhibited within the species groups and the considerable differences between groups. It was suggested that these similarities and differences are such that they may be sufficient for it to be possible to place a nest in a species group.

The discoveries of nests of *C. braunsi* and *C. toriger* have made it possible to add Group 3 to those groups (5 and 8) for which the nest characters of a group as a whole can be defined. It was suggested (Gess and Gess, 1988a) that Group 3 may prove to be distinct in that the cells are all excavated sub-vertically beneath the bulb. At that time, however, the nests of only two species (*C. jacoti* and *C. nigripennis*) of the four assigned to this group were known. In the present paper the nests of the remaining two species (*C. braunsi* and *C. toriger*) are described. That they also excavate their cells sub-vertically and that no species from another group has been found to exhibit this characteristic adds support to the suggestion.

Gess and Gess (1988a) further drew attention to the apparent constancy in choice of forage plant family within species groups, three groups and one sub-group seeming to obtain nest provision from Mesembryanthemaceae only, two groups from Compositae only and one sub-group from Leguminosae only. At the time records for all species in a group were available for groups 3, 5 and 8.

The presently added forage plant records for *C. toriger* and *C. braunsi* support the contention that the characteristic forage plant family of Group 3 is the Compositae.

The present first forage plant records for *C. caffer* and *C. metanotalis* with those previously recorded for *C. rex* (Gess and Gess, 1988a) make known the preferred forage plant family of all the species of Group 6, confirming a constant choice of plants of the family Compositae by this group.

Gess and Gess (1988a) on the basis of the morphology of the clypeus and nature of the forage plants divided Group 2 into two sub-groups, Group 2a being constituted of *C. cerceriformis* Saussure and *C. peringueyi* Brauns and Group 2b being constituted of *C. clypeatus* and *C. richardsi*. At that time the nest structure was known only for *C. cerceriformis*. In the present paper the nest structure of *C. clypeatus* is described. It is very similar to that of *C. cerceriformis* suggesting a close relationship between the species of the two sub-groups despite their differences in morphology and choice of provision.

As already stated in the ethological account above, morphologically *C. micheneri* does not readily fall into one of the eight recognized species groups as it shows morphological similarities with both Group 2 and Group 3. The nest structure and nature of the forage plant recorded in the present paper, however, indicate that it does not belong to Group 3 nor indeed to any of the other recognised species groups with the possible exception of Group 2. One of the morphological characters in which *C. micheneri* differs from the four species currently forming Group 2 is the rounded rather than spinose or at least bluntly angular propodeum. That this difference in propodeal form need not be of any great significance is suggested by the fact that species with both spinose and rounded propodea occur also in the ethologically very homogeneous Group 8. That the forage plant belongs to the family Leguminosae suggests a closer relationship with Group 2b than with Group 2a, the known forage plants of which belong to the families Leguminosae (*C. clypeatus*) and Mesembryanthemaceae (*C. cerceriformis* and *C. peringueyi*) respectively. Certain morphological

characteristics, in particular those pertaining to the clypeus, indicate that *C. micheneri* does not, however, fit satisfactorily in Group 2b. It is therefore suggested that it should be placed in a additional sub-group, Group 2c.

Clearly the discovery of the nests of *C. peringueyi* and *C. richardsi* and the forage plant of *C. richardsi* are required before further clarification of Group 2 will be possible.

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The herpetofauna of the offshore islands of South Africa and Namibia

by

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ABSTRACT

The herpetofauna of the continental offshore islands of South Africa and Namibia is reviewed. Historical and recent records are discussed and the origin and affinities of the herpetofauna are considered. A total of 23 species has been recorded from 11 islands. The greatest diversity (16 species) occurs on the largest island, Robben Island in Table Bay. The commonest island species are *Phyllodactylus porphyreus* (seven islands) and *Cordylus cordylus* (four islands). All of the islands have rocky coastlines and are unsuitable for nesting sea turtles.

The islands have been affected to different degrees by sea-level fluctuations associated with periods of glaciation. All were connected to the mainland during the last Glacial Maximum (16 000 BP). Human disturbance has occurred on all the islands and many species have been introduced. A number of islands have relict populations of some species, and these probably date from the time when the islands were connected to the mainland. No significant correlation exists between species richness and an island's size or its distance from the mainland. This is attributed to the relatively small size of the islands, their depauperate herpetofaunas, and the habitat requirements of the species. The spotted gecko *Pachydactylus maculatus* grows to a much larger size on St Croix Island than on the adjacent mainland but gigantism does not occur in reptile populations on other islands.

INTRODUCTION

The continental shelf of southern Africa includes a total of 69 small rocky islets and offshore islands (Skead, 1975). These range in size from small, wave-swept rocks that harbour a few resting seals or seabirds to the large and well-vegetated Robben Island that has been colonised for many years, albeit unwillingly, by the many inmates of the old leper colony, insane asylum and penal settlement (De Villiers, 1971). Almost all the islands are small and uninhabited. Only two islands exceed 100 hectares in size. Most were periodically visited by early settlers and seamen who came to collect food, skins and oil from the prolific colonies of seals and seabirds. Nowadays all of the islands are protected although accumulated guano is still harvested from some, particularly those along the Namibian coast. The larger islands (Robben, Dassen, Dyer and Bird islands) have lighthouses, some of which are now automated and require only periodic visits for maintenance. Human disturbance occurs regularly on most islands and some are permanently inhabited.

The islands may be conveniently grouped; those of Algoa Bay in the Eastern Cape (St Croix and Bird islands); those of the southwestern Cape (Robben and Dassen islands, and those associated with Saldanha Bay, i.e. Marcus, Malgas, Jutten, Meeuw and Schaapen islands); and those along the Namibian coast near Lüderitz Bay (Pomona and Possession islands). More isolated is Dyer Island, situated off the Bredasdorp coast, southern Cape. All the islands are situated on the continental shelf and have been affected by sea level changes during periods of glaciation. During the last Glacial Maximum (16 000 BP) sea levels were very low (approximately −130 m) and during this period all of the present islands along the southern African coast would have been joined to the mainland (Tankard, 1976). With the onset of warmer climates and the subsequent rise in sea level, the islands became progressively cut off from the mainland. Some very low-lying islands may have been affected by a brief and slight rise (3m) in sea-levels 2 000 BP during the last climatic optimum or hypsithermal (Flemming, 1977).

Variation in species richness of the major islands of the southwestern Cape has been analysed by Brooke and Crowe (1982). Alien species on all South African offshore islands have been reviewed by Brooke and Prins (1986) and Cooper and Brooke (1986). Although these authors list a number of reptiles from some islands, they do not comprehensively review old records (Brooke and Crowe, 1982, state explicitly that they have not consulted literature prior to 1971). The present account is the first detailed review of the herpetofauna of these islands and the first to consider origins and affinities.

The historical references derive mainly from Skead (1975). Recent literature was reviewed for references to reptiles and amphibians on the islands. Specimens from the islands housed in

the major herpetological collections in South Africa were recorded (see appendix for acronyms and catalogue numbers); other records, where noted in the literature, are given. Searches for reptiles and amphibians were made during trips by the author to a number of the major islands: Dassen Island, 4–10 April 1987 and 4 November 1988; Bird Island (Algoa Bay), 22–26 May 1980; St Croix Island (Algoa Bay), 7 July 1979 and 22 March 1989.

Historical and recent records of island species were assessed and compared to determine which were likely to represent introductions and which represent naturally occurring species. The latter may have reached the islands through rafting or may be relict populations from periods of sea-level fluctuations.

HERPETOFAUNA OF THE OFFSHORE ISLANDS

The geographical situations of the islands discussed are shown in Fig. 1, and the reptiles and amphibians recorded from the islands are listed in Table 1. Specific details for the islands and their recorded herpetofauna are given, prefaced by a short note on the marine reptiles found in the coastal waters of southern Africa.

A number of sea turtles (Hughes, 1974a and b) and a single sea snake occur. The yellow-bellied sea snake *Pelamis platurus* is common in Algoa Bay (PEM R 13, 61, 1128,1130–31, 1492, 2360), and there are sporadic records along the southern Cape coast as far as False Bay (Broadley, 1983). However, the species is excluded from the Atlantic Ocean by the cold Benguela Current that sweeps up the western Cape coast, bringing cold Antarctic waters close inshore. Although green sea turtles have recently been reported to bask on desolate beaches near the Cunene River mouth in northern Namibia (Tarr, 1989), the steep rocky shoreline of most of the southern African offshore islands precludes sea turtles from beaching. The shoreline of Bird Island is less steep but still rocky, although sea turtles do forage close inshore. A large (carapace length approximately 1 m) loggerhead sea turtle, *Caretta caretta*, was caught by a fisherman using squid bait from the Bird Island jetty on 24 May 1980, but was subsequently released (Branch, pers. obs.). None of the islands has sandy beaches suitable for nesting sea turtles, even though two species, *Caretta caretta* and *Dermochelys coriacea*, nest in northern Natal (Hughes, 1974a,b) and occasionally further south (Branch, 1988a). The only sea turtle record for any offshore island is a single hawksbill turtle, *Eretmochelys imbricata*, shell recorded from the beach of Dyer Island. The specimen was initially catalogued from Dassen Island but this was later corrected to Dyer Island. This is more likely in view of the cold Benguela Current on the west Cape coast.

St Croix Island, Algoa Bay (33° 48′S, 25° 46′E; 625 m × 250 m, 2.5 ha, 3.9 km from coast, 59.4 m a.s.l., not manned; Fig. 2.)

Hewitt (1920) noted that the common girdled lizard, *Cordylus cordylus*, was abundant on the island and presumed this to be due to the absence of predation by kestrels. He also noted that they were smaller, had narrower heads, and as adults lacked the bright brick-red colours of Grahamstown specimens. During a brief (3 hr) visit to the island by the author (21 March 1989), many *Cordylus cordylus* were seen basking on rocks or foraging around penguin nests (Fig. 3). The island is home to a major breeding colony of the Jackass penguin, *Spheniscus demersus*, and has a resident population of 13–18 000 individuals. Nine lizards were caught, weighed and measured. Numerous other specimens were seen, a number of which were slightly larger than any captured. The largest lizards measured (male, snout-vent (SV) 70 mm, tail 70 mm, weight

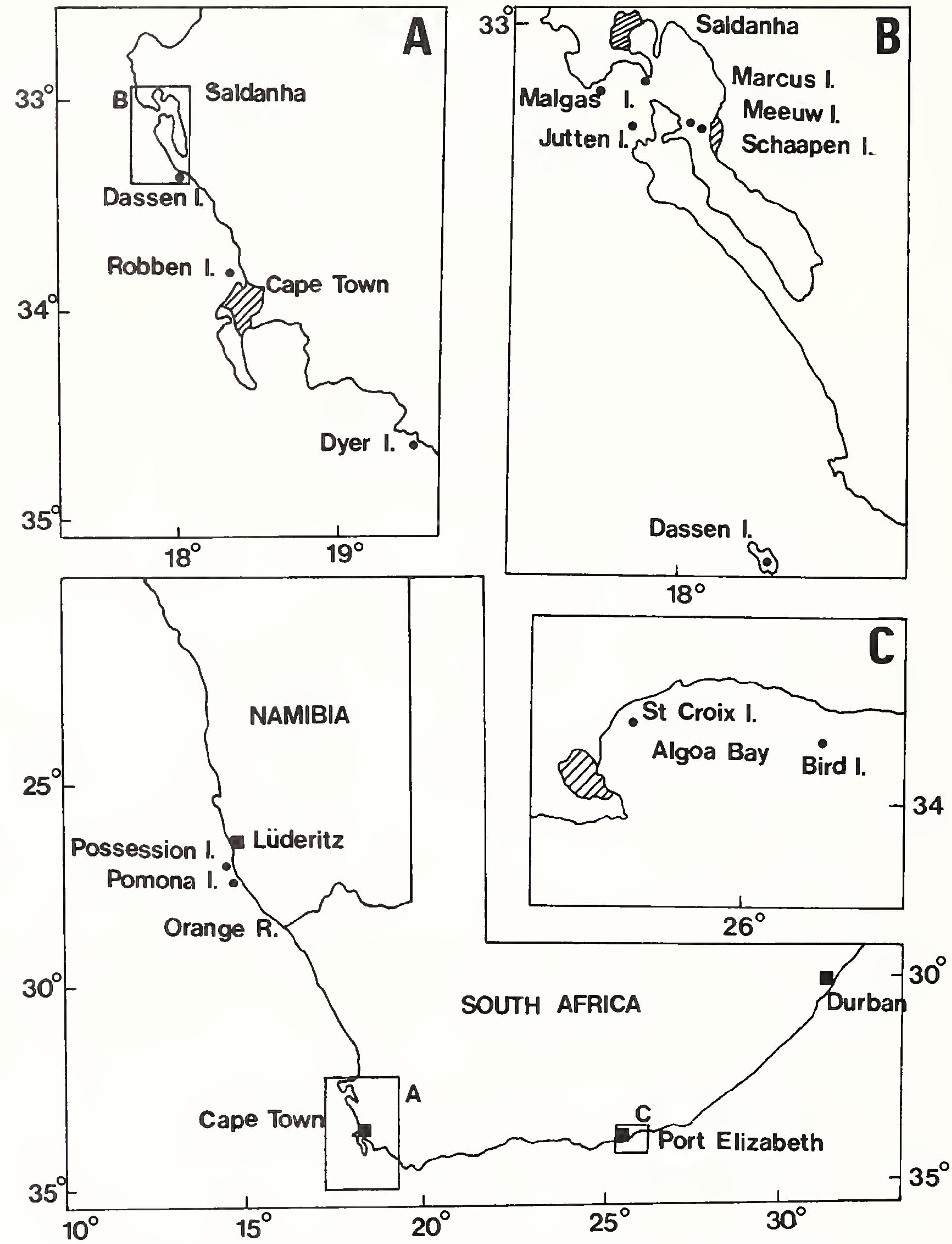

Fig. 1. Geographical location of the offshore islands of South Africa and Namibia.

Table 1.

Herpetofauna of the offshore islands of South Africa and Namibia

SPECIES	SOUTH AFRICAN AND NAMIBIAN OFFSHORE ISLANDS											
	1	2	3	4	5	6	7	8	9	10	11	**TOTAL**
Size of island (ha)	507	222	41	7	11	9	46	20	2.5	3	90	
Distance from coast (km)	6.7	9	0.5	0.14	1.2	0.8	0.8	7	3.9	0.2	2.7	
Human habitation	*	*			*	*	*	*			*	**7**
Amphibians												
Strongylopus grayii	*											**1**
Breviceps rosei	*											**1(?)**
Reptiles												
Snakes												
Pseudaspis cana	*											**1**
Lamprophis inornatus	*											**1**
Lycodonomorphus rufulus	*											**1**
Aspidelaps lubricus										?		**1(?)**
Lizards												
Gekkonidae												
Phyllodactylus porphyreus	*	*	*	*	*	*	*					**7**
Phyllodactylus lineatus			*	*								**2**
Pachydactylus maculatus									*			**1**
Pachydactylus geitje	*											**1**
Chamaeleonidae												
Bradypodion pumilum	*											**1**
Agamidae												
Agama atra		?										**1(?)**
Scincidae												
Mabuya capensis	*		*					*				**3**
Mabuya homalocephala	*											**1**
Scelotes bipes	*											**1**
Scelotes gronovii	?	*	*	*								**3(4?)**
Acontias meleagris	*		*				*					**3**
Cordylidae												
Cordylus cordylus	*		*				*		*			**4**
Tetradactylus seps	*											**1**
Chelonians												
Eretmochelys imbricata								*				**1**
Chersina angulata	*	*						*			*	**4**
Geochelone pardalis	*											**1**
Pelomedusa subrufa											?	**1(?)**
TOTAL (excluding doubtful records)	**16**	**3**	**6**	**3**	**1**	**1**	**3**	**3**	**2**	**0**	**1**	

Southwestern Cape	1, Robben Is; 2, Dassen Is.; 3, Schaapen Is., 4, Meeuw Is., 5, Marcus Is.; 6, Malgas Is., 7, Jutten Is., 8, Dyer Is.
Algoa Bay	9, St Croix Is.
Namibia	10, Pomona Is.; 11, Possession Is.

Fig. 2. St Croix Island, Algoa Bay, South Africa.

11.7 g; female SV 72 mm, tail 74 mm, weight 11.5 g) were not significantly smaller than specimens on the adjacent mainland (Branch, unpubl. obs.). They are a dull dark brown in coloration. Their relationship to typical *Cordylus cordylus* and to the more arboreal, closely-related species *Cordylus tasmani*, which is endemic to the Valley Bushveld thicket of the adjacent Algoa Basin, needs to be investigated further. Pending the results of such a study, the population on St Croix is provisionally referred to typical *Cordylus cordylus*.

Hewitt (1920) also recorded the spotted gecko, *Pachydactylus maculatus*, from the island, noting that it was less abundant than the girdled lizard. During a visit to the island (22 March 1989) the author found six geckos sheltering among stone piles on the barren island. Two were recent hatchlings. The other four were adult females and were very large and had short, regenerated tails (snout-vent 55–60 mm, mean 58.00 mm; tail 27–31 mm, mean 29.25 mm; weight 7.19–7.53 g, mean 7.32 g). Eight preserved specimens, three females and five males, from the island support these findings. The females all measure over 50 mm SV (50–56 mm) and the males range from 38–53 mm SV. In a study of the spotted gecko on the adjacent mainland 253 specimens were weighed and measured. Females grew larger than males: largest male, SV 41mm, weight 2.6g; largest female, SV 42 mm, weight 3.1 g. Even the largest mainland female weighs less than half that of the smallest St Croix female, and the size of males is also much smaller. These results demonstrate that the geckos on St Croix grow substantially larger than on the adjacent mainland. Whether this is due to reduced predation or abundant food is unknown.

Of the six live geckos collected all but the smallest hatchling had regenerated tails. Similarly all eight preserved geckos have regenerated tails. The incidence of regenerated tails on the island is therefore very high (91.67%). Tail regeneration frequency on the mainland was found

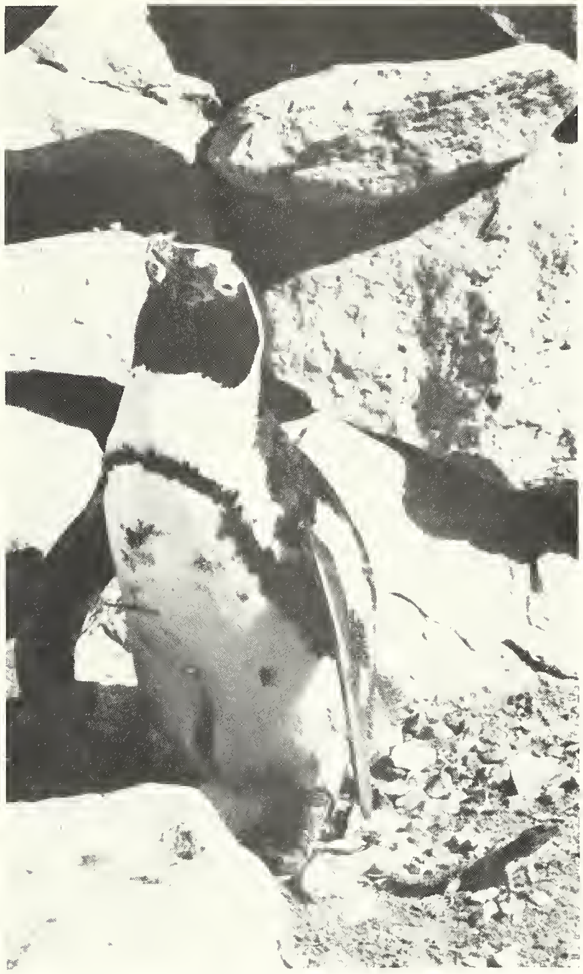

Fig. 3. The common girdled lizard *Cordylus cordylus* foraging among nesting Jackass penguins on St Croix Island, Algoa Bay, South Africa.

to be dependent upon age. All geckos over 40 mm SV had regenerated tails. Tail autotomy in geckos is usually considered to serve as an antipredator device although tail-loss may occur for other reasons (Arnold, 1988). Some geckos on the mainland were observed to undergo 3–4 tail regenerations; a principal predator was found to be the Natal hunting spider, *Palystes natalius* (Branch, unpublished data). Snakes are also often considered to be major predators of lizards. The potential efficacy of tail autotomy was noted when a spotted skaapsteker, *Psammophylax rhombeatus* was found to contain a complete spotted gecko and the autotomised tail of another spotted gecko (Branch and Braack, 1987). The cause of the high frequency of tail loss in spotted geckos from St Croix is unknown as the normal predators (snakes, viverids, large spiders, etc.)

Fig. 4. Size difference between populations of the spotted thick-toed gecko, *Pachydactylus maculatus*, from St Croix Island, Algoa Bay (right), and the adjacent mainland (left).

are absent from the island. Penguins, which were observed to peck at girdled lizards that came to close to their nests, may be responsible for some tail loss. Whether the nocturnal spotted gecko is treated in the same manner is unknown. Intra-specific fighting may also be responsible for some tail loss but it is unlikely to be solely responsible for the high percentage observed.

Bird Island, Algoa Bay (33° 51′S, 26° 17′E; 548 m × 320 m, 19 ha, 8.4 km from coast, 9.1 m a.s.l., manned)

No early visits to the island mention the presence of reptiles on the island (Skead, 1975) and Hewitt (1937) observed that "On Bird Island there are no reptiles whatever". However, Rand (1963) stated ". . . lizards, tortoises and occasionally snakes are found here too". There are no preserved voucher specimens in any museum collection to validate this claim. Jordan, ex-lighthouse keeper on Bird Island, 5 Dec 1951—24 Jan 1953, records (*in litt.* Skead, April 1971) that "There were lizards on the island, also one tortoise, small type. My children collected a few on my brother-in-law's farm and took them over for company for him. There were no snakes . . . There were also a few frogs, mainly brought over with our vegetables . . . my brother-in-law . . . used to dig out cabbages, carrots . . . [etc.] . . . intact and we used to replant them on Bird Island". The identity and the fate of these animals are unknown. The Port Elizabeth Museum has had an active research program studying the gannet population on the island for the last ten years. During this period, of almost monthly visits, no reptiles or amphibians have been discovered living on the island. In 1981, an angulate tortoise was found freshly dead on the shore of Bird Island (A. Batchelor, pers. comm.) following heavy rain on the

mainland. The old records noted by Rand (1963) can either be discounted or they document temporary colonizations that have subsequently died out.

Dyer Island, Southern Cape (34° 40′S, 19° 25′E, 731 m × 180 m, 20 ha, 3.5 km offshore, 6 m a.s.l., manned)

Brooke and Crowe (1982) record the Cape skink *Mabuya capensis* and the angulate tortoise *Chersina angulata* from the island but give no further details. Symons (1924) visited the islands to collect bird eggs but records no observations of tortoises, suggesting that these introductions may have occurred recently, perhaps in a similar manner to that noted above and by Haacke (1965) for Possession Island (see below).

Robben Island, South-western Cape (33° 49′S, 18° 22′E; 4 km × 2 km, 507 hec., 7 km from land, 30 m a.s.l, colonised since 1652)

Robben Island is the largest South African offshore island and also the closest to Cape Town which was one of the first areas on the subcontinent to be settled by Europeans. It has been continuously inhabited since 1652 and has been substantially altered by more than 300 years of human occupation. In the 19–20th century it was used as a leper colony and insane asylum (both of which have now been closed). It has been used as a penal colony from the earliest days (Thunberg, 1793, notes that "criminals [are] exiled there"). At present access to the island and possibilities for biological surveys there are restricted.

Amphibians

Robben Island is the only offshore island from which an amphibian has been recorded (i.e. the spotted stream frog, *Strongylopus grayii*) (Rose, 1950). The species was recently confirmed to be present at the old quarry (Baard, *et al.*, 1986). This, the only permanent source of freshwater on the island, dates from the settlement established by Van Riebeeck in 1652. Due to their intolerence of salt water amphibians do not easily colonise off-shore islands. However, *S. grayii* is common in the southern Cape coastal regions and can be found breeding in pools of freshwater in the dune slacks. It is probable that the species was introduced to Robben Island by man, possibly in a manner similar to that noted for frogs to Bird Island in Algoa Bay (see above). That the spotted stream frog can be successfully translocated is shown by its introducition to St Helena in the middle of the Atlantic Ocean (Frost, 1985).

The absence of standing fresh water need not preclude all amphibians, development in some terrestrial species being direct. Such a reproductive mode is characteristic of rain frogs (*Breviceps* spp.), which are common in the Cape coastal region. Poynton (1964) records Rose's rain frog (*Breviceps rosei*), a species restricted to the sandveld of the western Cape coastal foreland where it may be locally common, from the island. This record is based on three specimens in the South African Museum. It should be noted that these specimens and that of the olive water snake from Robben Island (see below) were donated (collected ?) by Rev. G. Fisk and accessioned into the SAM collection between 1895 and 1896. Boulenger (1910) does not record any amphibians from Robben Island and furthermore no recent collections of *B. rosei* confirm the presence of the species on the island.

Reptiles

Numerous reptiles have been recorded from the island but it is difficult to determine which species have been introduced during the period of human settlement. However, early records do give some idea of the island's relatively diverse herpetofauna before European settlement. The

indigenous Khoisan population did not use boats at sea and there is no evidence that they visited any of the offshore islands. They were thus not responsible for herpetological introductions.

Snakes

The earliest references note the presence of snakes on Robben Island:

1610 "Upon the Illand be . . . [an] aboundance of great snakes lying upon the ground against the Sune . . ."—Thomas Best (in Raven-Hart, 1967).

1614 ". . . the iIlande is very full of Snakes . . ."—Nicholas Downton (in Raven-Hart, 1967)

1615 ". . . there are a very great number of snakes in that island . . ., so many of them venomous worms that a man cannot tread safely in the long grass which grows in it for fear of them . . ."—Edward Terret (in Raven-Hart, 1967)

Such is the universal fear of snakes that soon attempts were made to eradicate them from the island.

1638". . . the blacks while there had destroyed almost all the penguins and the snakes."—Arthur Gijsels (in Raven-Hart, 1967)

1654 ". . . there are snakes which we notice do them (i.e. the sheep) no harm, and of these our men are instructed to exterminate as many as possible"—Van Riebeeck (in Thom, 1952–1958)

1658 "You must make every effort to destroy the numerous snakes during periods of idleness, so that the island may once and for all be cleared of these poisonous vermin."—Van Riebeeck (in Thom, 1952–1958)

That these attempts were unsuccessful is indicated by Le Vaillant's comment in 1782 quoted by Skead (1975) that he had

". . . seen here a great many black serpents four feet (1.21 m) in length but they are not venomous . . ."

More recently Siegfried (*in litt.* Skead, November 1965) noted that when the Cape Department of Nature Conservation wanted mole snakes to restock the Cape Peninsula in order to control small rodents they "took gangs of men over to Robben Island and found a mole snake under every pile of rubbish they turned up."

The first identifications of snake species from the island, based on specimens housed in the South African Museum, are by Boulenger (1910). He records the brown water snake *Lycodonomorphus rufulus* and the olive house snake *Lamprophis inornatus*. FitzSimons (1962) repeats these records and also includes the mole snake *Pseudaspis cana*. It is surprising that Boulenger did not document this large, non-venomous colubrid as it fits best the early descriptions of snakes on the island (e.g. 'great size', 'black'). Specimens from the western Cape populations of this impressive snake are often a uniform black and grow much larger than those from elsewhere (in excess of 2 m; Broadley, 1983). The mole snake was probably present before settlement by man. It is possible that the other species were also present but overlooked as both are small and nocturnal. Small mammals form the usual diet of the olive house snake although this species will also take small reptiles (Branch, 1988). The brown water snake feeds almost exclusively on frogs but may occasionally take fish and exceptionally geckos. Its existence on the island is probably dependent upon the presence of amphibian prey.

Lizards

Very early references note the presence of chamaeleons and other lizards on the island:

1620 "There are . . . also some chamaeleons and other lizards"—Augustin de Beaulieu (in Raven-Hart, 1967)

1773 "Now a resort of chamaeleons and quails."—Thunberg (in Skead, 1975).

Boulenger (1910) includes Robben Island as a locality for a number of lizards, based on specimens in the South African Museum, but gives no further information on their origin or details of their capture. These are:

Ocellated gecko, *Pachydactylus geitje* (as *P. ocellatus*)

Cape girdled lizard, *Cordylus cordylus cordylus* (as *Zonurus cordylus*)

Redsided skink, *Mabuya homalocephala homalocephala*

Silvery dwarf burrowing skink, *Scelotes bipes*

Cape legless skink, *Acontias meleagris meleagris*

Short-legged seps, *Tetradactylus seps*

Rose (1926 and 1929) records a number of additional lizard species from the island, as well as giving notes on the above species:

Marbled leaftoed gecko, *Phyllodactylus porphyreus*

". . . very common . . . on Robben Island".

Ocellated gecko, *Pachydactylus geitje* (as *P. ocellatus*).

". . . may be seen in very large numbers on Robben Island",

". . . closely associated with *Zonurus cordylus, Phyllodactylus porphyreus* and *Acontias meleagris*."

Cape girdled lizard, *Cordylus cordylus cordylus*

"On Robben Island yellow-brown ones (flavus) are extremely numerous in the stone heaps . . . but no black ones (niger) were seen."

Silvery dwarf burrowing skink, *Scelotes bipes*

"A specimen we obtained from Robben Island produced two active young . . . during . . . March."

Cape legless skink, *Acontias meleagris*

"On Robben Island it is particularly abundant and we once obtained nine specimens in little over an hour by turning over large stones by the side of the road that skirts the island."

FitzSimons (1943) records most of these species and adds the Cape dwarf chamaeleon, *Bradypodion pumilum* (as *Microsaura pumila pumila*), based on a specimen in the Albany Museum.

Baard *et al.* (1986) in a recent survey of the island confirm the presence of eight of the above species, including the mole snake, and also document the presence of the Cape skink *Mabuya capensis* (two were preserved and nine others observed). As the survey occurred during the dry summer, the presence of other amphibian species on the island could not be determined.

Bustard (1963) records reproduction in 50 captive ocellated geckos received from Robben Island. Mouton (1987) discusses the relictual distribution of melanistic girdled lizards, *Cordylus cordylus*, in the southwestern Cape and confirms Rose's record of the typical form on Robben Island and the presence of the melanistic *C. c. niger* on Jutten Island and Schaapen Island in the Saldanha Bay area. Mouton *et al.* (1987) include Robben Island as a locality for *Scelotes gronovii*

prior to 1978 but give no further indication of the provenance of this record and exclude it from their present distribution map. The record is repeated in Baard (1988). It is based on a specimen in the Transvaal Museum the identity of which has been confirmed (W.Haacke, pers. comm.). The species is not known from the adjacent mainland and may either be mis-labelled or represent a northern retraction of the species' range following separation of the island from the mainland. During a recent search on the island the only fossorial skinks found were *Scelotes bipes* and *Acontias meleagris* (Baard, pers. comm.). Further searches on the island are required to resolve the issue.

CHELONIANS

Tortoises are mentioned in the earliest references to Robben Island:

1503 "On this island they killed many birds, . . . and sea wolves and tortoises, of which there is great abundance."—Antonio da Saldanha (in Raven-Hart, 1967).

These have not been discussed by recent authors (Skead, 1975). It is probable that they are the angulate tortoise. The presence of the angulate tortoise on the island was confirmed by Baard *et al.* (1986). As in many other places in the south-western Cape, the leopard tortoise *Geochelone pardalis* has been introduced to Robben Island. D'Ewes (1967) noted that in 1959 a police launch had discovered an adult leopard tortoise swimming in the sea "a couple of miles offshore from Robben Island, and swimming strongly for the mainland." Skead (1975) has traced the origin of this specimen to one of 25 tortoises taken to the island from the Paarl Roller Flour Mills (now SASKO) in 1959. They had been kept as pets by workers at the mill, and were disposed of to Robben Island (C. W. van der Westhuizen *in litt.* Skead, 3.3.1971). This species was not present during the survey of Baard *et al.* (1986).

Dassen Island, Southwestern Cape (33° 26′S, 18° 05′E; 2.5 km × 1.05 km, 222 ha, 9 km offshore, 19 m a.s.l, manned)

Records of early visits to the island note the abundance of wildlife, e.g. both Sir Edward Michelbourne, 1601 (in Raven-Hart, 1967) and Van Riebeeck, 1652 (in Thom, 1952–8) comment on the "unbelievable multitude of seals, black birds (cormorants) and penguins.". They also noted the presence of a 'rabbit'; in fact the rock hyrax or dassie *Procavia capensis*. The island's early name, i.e. Cony Island, and its present name are based on the presence of this species on the island. They were later eradicated and were replaced with the European rabbit *Oryctolagus cuniculus* which was introduced as food late in the administration of the Cape by Van Riebeeck (1652–1662). There are no early records of any reptiles or amphibians. Four reptile species have been reported in recent years although only three are recently confirmed.

Boulenger (1910) includes Dassen Island as a locality for *Agama atra* and *Scelotes gronovii*, based on specimens in the South African Museum but he gives no further information on the specimens. FitzSimons (1943) repeats the record for the rock agama but with no further documentation or proof that a viable population existed on the island. These rock-living, diurnal, and brightly-coloured (at least in males) lizards are highly visible but no evidence of their presence on the island was found during the author's recent visits nor has any evidence of their presence been reported subsequently. Rose (1929) records receiving a specimen of *Scelotes gronovii* from Dassen Island but does not mention the rock agama.

During the author's first trip to the island (4–10 April 1987), 12 *Scelotes gronovii* were collected in sandy, gritty soil under cover (granite slabs, old corrugated iron sheets, wooden logs, etc.), some only a few metres above the high water mark and others among the roots of

scrub vegetation. All were adults (N = 11, SV 65–82, mean 73.44 mm), and all but the two smallest (SV 65–67 mm) had regenerated tails (i.e., 81.82%). Specimens from Elands Bay and Langebaan on the adjacent mainland are slightly smaller in size (N = 5, SV 61–77 mm, mean 66 mm) but there are too few specimens to determine whether this size difference is statistically significant. Two young were born whilst the above specimens were retained in a collecting bottle but it was not possible to determine whether they came from the same or separate mothers. They measure; 1. 40 + 21 mm (SV + tail); 2. 38 + 12 (tail broken). In adults with original tails the tail ranges from 74.3–93.8 % (mean 84.5%, n = 5) of the SV length. This contrasts with 52.5–73.6 % (mean 62.0 %, n = 3) in new born specimens, indicating that tails are relatively smaller in juveniles than adults.

McLachlan (1978) queried the safety of this species on Dassen Island following disturbance during guano collection. However, little guano collecting now occurs on the island and is restricted to the northern, barren peninsulas. The dwarf burrowing skink is distributed throughout the island in areas not disturbed by guano collecting. The species is still included in the revised *South African Red Data Book—Reptiles and Amphibians* and, although not currently threatened, is placed in the Restricted category (Branch, 1988c).

Neither Boulenger (1910), FitzSimons (1943) nor Rose (1929, 1950 and 1962) records the presence of the marbled gecko *Phyllodactylus porphyreus* on Dassen Island, even though FitzSimons (1943) does record the species from Robben and Jutten islands. Its presence on Dassen Island was first documented by Brooke and Crowe (1982), however, no further details were given or voucher specimens documented. Numerous specimens of the marbled gecko were found by the author during a short trip to the island (4–10 April 1987). Twenty one specimens were found sheltering under a single granite flake (*c* 35 cm × 40 cm) on granite bed rock, 50 m NW of the lighthouse on 7 April 1987. Another nine geckos were sheltering under a slightly larger slab in the same region. Another granite slab, partially embedded in sandy soil in the centre of the island, sheltered three geckos. An additional four geckos were found individually sheltering under stones or building debris around the keeper's house.

The SV and tail length of 29 geckos were measured, and the state of regeneration of their tails noted. The development of eggs or enlarged endolymphatic sacs (ELS) in the neck region of females was also recorded. Adult males are easily sexed by the prominent hemipeneal bulge at the base of the tail. The sex ratio was 0.69 (11:16 M:F). Very few juveniles were found. No females had obvious well-developed eggs but 5 had well-developed ELSs. Craye (1976) notes that females produce two eggs in spring and that ELS development occurs in late winter to meet the stress of rapid calcification of eggs-shells in spring. Two geckos lost their tails during capture. Of the remaining 27 geckos 14 (51.85%) had regenerated tails. Craye (1976) observes that tail autotomy is well-developed in the marbled leaftoed gecko but gives no details of frequency. The number of Dassen Island geckos with regenerated tails, in a situation where many of the normal predators (e.g. snakes) are absent is relatively high. However, the spotted gecko on St Croix Island also has a very high tail break frequency, that may be caused by pecks from penguins defending their nest sites.

The date of introduction of the angulate tortoïse, *Chersina angulata* to Dassen Island is undocumented. In numerous early references to the island (from 1601 onwards) there is no mention of tortoises (Skead, 1975). This contradicts the conclusion of Brooke and Prins (1986) that the species is "probably indigenous". The first record of tortoises occurs as an appendix in Rose (1929), who notes that "*Testudo angulata* is plentiful on Dassen Island, having probably

been introduced somewhat recently from the mainland." Sclater (1896) makes no reference to tortoises on the island during a visit in 1896, which indirectly supports Rose's comment. It is now known to be present in high densities on the island.

Studies by Apps (1983) and Berruti (1986) on the impact of feral cats on the the island's fauna revealed only minimal predation on the reptiles. Small cats were found to occasionally take *Scelotes gronovii* (<1% prey mass), but no tortoise or gecko remains were present in numerous scats or gut contents studied. The feral cats on the island have recently been eradicated (Berruti, 1986) to protect the endangered jackass penguin colony.

Marcus Island, Saldanha Bay (32° 02′S, 17° 58′E; 650 m × 200 m, 11 ha, 1.2 km offshore, 7.3 m a.s.l., usually manned)

Brooke and Crowe (1982) record *Phyllodactylus porphyreus* from the island but give no further details. The record postdates the connection of the island to the mainland by a causeway in 1977. It is possible that the gecko colonised the island via this land connection.

Malgas Island, Saldanha Bay (33° 03′S, 17° 55′E, 300 m × 300 m, 9 ha, 800 m offshore, 7 m a.s.l., manned)

The only herpetological record from the island is that of two adult and one juvenile *Phyllodactylus porphyreus* collected 25 January 1951 by the Swedish Expedition to southern Africa (FitzSimons, 1957).

Jutten Island, Saldanha Bay (33° 05′S, 17° 57′30″E, 1550 m × 650 m, 46 ha, 800 m offshore, 60.5 m a.s.l., manned)

FitzSimons (1943) records *Phyllodactylus porphreus* and *Cordylus cordylus* from the island and both species were also collected there by the Swedish Expedition to southern Africa (FitzSimons, 1957). Brooke and Crowe (1982) also record *Acontias meleagris*. Mouton (1987) notes that the population of the girdled lizard on the island is referable to the melanistic form (niger).

Meeuw Island, Saldanha Bay (33° 05′S, 18° 00′30″E, 500 m × 300 m, 7 ha, 140 m offshore, 9 m a.s.l., not manned)

McLachlan (*in litt.* to Skead, April 1971) records *Phyllodactylus porphyreus* and *Scelotes gronovii* from the island, whilst Brooke and Crowe (1982) also record *Phyllodactylus lineatus*.

Schaapen Island, Saldanha Bay (33° 06′S, 18° 01′E, 650 m × 600 m, 41 ha, 500 m offshore, 18 m a.s.l., not manned)

Lichtenstein in 1803 noted that "the inhabitants of this as well as the other islands are chiefly sea-fowl, serpents and lizards" (quoted by Skead, 1975), and later Symons (1926) recorded that ". . . Schapen has a very bad reputation for snakes, cobras and puff-adders being said to be very plentiful". However, this has not been confirmed recently, and Grindley (*in litt.*, Skead, April 1971) found that "Some years ago I did some work on Schaapen island in Saldanha Bay where I found *Cordylus cordylus* to be common and the burrowing lizard *Acontias meleagris* to be present." Similarly, Brooke and Crowe (1982) record the lizards *Phyllodactylus lineatus, Scelotes gronovii* and *Mabuya capensis* on the island. The *Scelotes gronovii* are of typical size (N = 6, SV 60–74 mm, mean 68.83 mm), not noticeably larger than those on the adjacent mainland.

Pomona Island, Namibia (27° 12′S, 15° 16′E, 91 m × 366 m, 3 ha, 200 m offshore, 2.5 m a.s.l., not manned)

This small, barren guano island lacks vegetation or permanent water. Nonetheless, Bogert

(1940) records a single specimen of the Coral snake *Aspidelaps lubricus lubricus* from the island. Mertens (1954 and 1955) transferred this specimen to his newly-described race, *A. l. infuscatus*, subsequently followed by FitzSimons (1962). However, Broadley (1983) does not list this specimen in his revision although he makes no further comment on its identity or provenance. It should be noted that Bogert (1940), in his original description of the specimen, records that "The stomach of this snake contained a small unidentified rodent and nineteen eggs, presumably of some lizard. The eggs measure approximately 10 mm × 6 mm, with soft shells, typical of many species of gecko". No southern African gecko has soft-shelled eggs and no geckos have been recorded from Pomona Island. The small size and barren nature of the island make it a most unlikely habitat for this nocturnal, semi-fossorial elapid and it is probable that the specimen was collected elsewhere.

Loveridge and Williams (1957) record an angulate tortoise from Pomona, based on a specimen in the AMNH. It is not known whether this specimen came from the adjacent mainland or the island to which it might have been taken by a guano worker. It is pertinent that whereas FitzSimons (1950) lists a number of other specimens from Pomona it is obvious from his text that he refers to the mainland adjacent to Pomona Island in Lüderitz District. Specimens of the angulate tortoise are still found around Lüderitz Bay, probably having escaped from captivity. The nearest natural population occurs 220 km to the south at Oranjemund (Branch, 1989).

Possession Island, Namibia (27° 01′S, 15° 12′E; 5.6 km × 0.8 km, 90 ha, 2.7 km offshore, 20 m a.s.l., manned)

This is the largest of the guano islands off the Nambian coast. It has a sparse scrub cover. Werner (1910) recorded one male and three female marsh terrapins (*Pelomedusa subrufa*) from the island but queried the record. Haacke (1965) discounted the record, noting that the small island contains no standing water and that the original collector (L. Schultze) made no reference to this unusual discovery in his account of his journey. During a two day visit to the island (May, 1963) Haacke found no evidence of the marsh terrapin but did note the presence of two angulate tortoises "brought from the Cape as pets". The permanent resident supervisor also noted that "the only wild reptiles ever noticed were the odd skink and gecko found amongst timber or empty bags from Cape Town" (Haacke, 1965).

RECENT GEOLOGICAL HISTORY OF THE ISLANDS

All the offshore islands discussed in this paper occur on the continental shelf and are relatively close to the South African mainland (maximum distance 9 km offshore). All have been affected, to a greater or lesser degree, by sea level fluctuations associated with periods of glaciation. Tankard (1976) has reviewed sea level fluctuations in the region during the Cenozoic. He notes a rapid fall in sea-level with the advance of the final Würm glaciation (17–18 000 BP) and a minimum sea level 130 m lower than present. At this time all of the South African offshore islands would have been connected to the mainland. Following the maximum glacial advance, the rate of retreat of the ice was nearly constant. The present level was reached about 6500 BP. This infers a sea-level rise of some 1.125 m per 100 year for the period 18 000—6500 BP. The islands are separated from the mainland by water of different depths. Most channels are under 20 m deep. The maximum depth (approx. 40 m) occurs between Ysterfontein and Dassen Island (which is also the farthest offshore). This island would thus have separated from the mainland

about 14–13 000 years BP, whereas the islands with the shallowest channels (i.e. those of Saldanha Bay, and Pomona (9 m) and Possession (12.8 m)) would have separated between 8–7000 BP. The Algoa Basin islands are separated from the mainland by water of depths of 17–23 m and would thus have separated 10–9000 BP.

During the last climatic optimum or hypsithermal, which ended *c* 2000 years ago, sea levels were at least 3 m higher than at present (Flemming, 1977). At this time many of the low-lying islands (e.g. Bird Island, Algoa Bay; Dyer Island; and Pomona Island, Namibia) even if still exposed, would have been seriously affected by storm swells. They now either lack a herpetofauna or have one only recently introduced.

INTRODUCED SPECIES

The larger islands have a longer and more intense history of human habitation and there has therefore been a greater chance for species introductions, be they deliberate or accidental. Tortoises are the only group for which evidence of deliberate introduction is known: *Chersina angulata*, Dyer Island, after 1924; Bird Island (Algoa Bay), 1951–3; Possession Island, 1960–3; *Geochelone pardalis*, Robben Island, 1959. It is highly likely that the colony on Dassen Island was deliberately introduced between 1896 and 1929.

It is difficult to determine which of the remaining species on the offshore islands represent accidental introductions. It is possible that many of the species recorded from Robben Island were present naturally before colonization by European settlers. The early records confirm the presence of snakes, chamaeleons, lizards and tortoises. Mouton and Oelofsen (1988) present a model explaining the distribution of melanistic girdled lizards in the region and note the importance of mountains as refugia for melanistic populations during the current amelioration of the climate following the last Glacial Maximum (16 000 BP). It is proposed that the rapid warming of the climate along the coastal lowlands since 14–12 000 BP allowed the typical form to rapidly expand its range and to colonize Robben Island before it became separated from the mainland. Whether at this period the species also managed to colonize St Croix Island in Algoa Bay is not known. The species is common in many coastal regions of the Cape Province (Burrage, 1974), particularly in the southwestern and Eastern Cape.

The same events probably allowed the burrowing skinks *Acontias meleagris* (Robben, Schaapen and Jutten islands), *Scelotes gronovii* (Robben (?), Dassen, Schaapen, and Meeuw islands) and *S. bipes* (Robben Island) and Rose's rain frog *Breviceps rosei* (Robben Island) to colonise a number of the islands on the southwestern Cape coast. It is extremely unlikely that so many islands could subsequently be colonised by small, fossorial lizards and a terrestrial, burrowing frog following separation from the mainland. It is equally unlikely that they could reach the islands by natural rafting or be accidentally introduced by man. They are therefore likely to represent relict populations, isolated following the rise in sea-level. The comments in Haacke (1965), concerning the introduction of geckos and skinks to Possession Island with cargo from Cape Town, offer a probable explanation for the presence of *Phyllodactylus porphyreus* on so many islands in the southwestern Cape and for the presence of the Cape skink *Mabuya capensis* on Dyer Island. The marbled leaftoed gecko is common throughout the coastal regions of the southern Cape and is very common in human habitations (Branch, 1988b). The introduction of geckos to ports in ship cargo is well-established (e.g. Branch, 1987; Loveridge, 1961).

When discussing Robben Island, it was noted that no permanent freshwater source existed on the island until the colony was established by Van Riebeeck in 1652. It is thus likely that the spotted stream frog *Strongylopus grayii* was introduced during the period of human settlement and that the brown water snake *Lycodonomorphus rufulus* which feeds on amphibians was also subsequently introduced.

The slight rise (3 m) in sea-level during the last hypsithermal (Flemming, 1977) may account for the current absence of reptiles on Bird Island in Algoa Bay, Dyer Island (where the herpetofauna is probably all introduced), Marcus and Malgas islands in Saldanha Bay (where the only record for both islands is the marbled leaftoed gecko which has probably been introduced), and Pomona Island, Namibia. All are low-lying islands and, although they would still have been exposed during the hypsithermal, they would have been drastically affected by storm swells.

Among the species that have been introduced to the offshore islands, a number have been translocated even further distances. The small stream frog, *Strongylopus grayii* has become established on St Helena (Frost, 1985). Loveridge (1947) notes a record of the ocellated gecko *Pachydactylus geitje* from Ascension Island but does not mention it in subsequent papers on the introduced herpetofauna of the island (Loveridge, 1959 and 1961). The specimens may have been mislabelled or the population may subsequently have died out.

ISLAND-SPECIES RICHNESS RELATIONSHIPS

The islands for which a herpetofauna has been identified were studied to determine whether a relationship between species richness and island size/distance from the mainland exists. Marcus Island was excluded from the analysis as it was connected by a causeway to the mainland in early 1977. The only record from the island (the gecko *Phyllodactylus prophyreus*) (Brooke and Crowe, 1982) occurs after the causeway was constructed. The species could have invaded the island naturally after connection to the mainland. The islands of Dyer, Pomona and Possession have also been excluded because in all cases the recorded reptiles have probably either been deliberately or accidentally introduced, or mistakenly assigned to the island. The angulate tortoise on Dassen Island and the leopard tortoise on Robben Island are introduced species and have been excluded from the following anlaysis.

Linear and log-log simple regression models (Sokal and Rohlf, 1969) were computed to test statistical relations between island herpetofauna richness and island area and distance offshore. Log/log plots for species/island area and species/distance offshore revealed no significant correlation. Brooke and Crowe (1982) found a highly significant relation between South African offshore island area and species richness for the total biota and also for various higher taxonomic categories (vertebrates, birds and plants). They found no significant relation in these categories between island species richness and island distance from the mainland. The absence of any significant correlation for the herpetofauna can be attributed to a number of factors: a) the small size of the islands (only two exceed 100 ha in extent); b) the depauperate herpetofauna which on most islands is restricted to 1–3 species; c) the low mobility of many reptiles and amphibians; d) the low salinity tolerance of most amphibians; and e) the lack of freshwater and thus suitable breeding sites for most amphibians.

RAFTING AND THE EFFECT OF FLOODS ON REPTILES AND AMPHIBIANS

It is often proposed that species may reach offshore islands by rafting. Arnold (1976) has discussed the history of fossil reptiles on Aldabra Atoll which has been inundated by rising sea

levels on at least two occasions. The giant land tortoise *Geochelone elephantina* has colonised the atoll on three occasions and it is probable that it originated from the northern areas of Madagascar. This large tortoise may either enter the sea voluntarily to cool itself or is washed out to sea by floods. It floats easily in water and could have drifted northwards in sea currents to wash ashore on Aldabra. This ability is well-illustrated by the discovery of a large leopard tortoise, *G. pardalis*, alive and well, drifting in the sea about 4 km offshore between Robben Island and the mainland (D'Ewes, 1967). The small land tortoises of South Africa, including the angulate tortoise *Chersina angulata* and the genera *Homopus* and *Psammobates*, are unable to swim (Branch unpubl. obs.) and can only colonise islands by rafting on flotsam in association with floods.

The effects of floods on reptiles and amphibians have rarely been documented but some indication of their impact may be judged by the following record. During the period 22–24 August 1971 the Port Elizabeth region experienced heavy rains and the Gamtoos, Swartkops and Sundays rivers flooded. Afterwards local newspapers recorded the capture of 93 snakes sheltering among debris on the beaches at the river mouths. The common slug eater *Duberria lutrix* was the most common snake. Other reptiles caught included the puffadder *Bitis arietans*; sand snakes *Psammophis* spp.; the skaapsteker *Psammophylax rhombeatus*; the night adder *Causus rhombeatus*; house snakes *Lamprophis* spp.; the garter snake *Homoroselaps lacteus*; the aurora house snake *Lamprophis aurora*; the Cape cobra *Naja nivea*; and at least 100 unidentified tortoises (Ross, *in litt.* to Skead, Sept 1971).

Although no tortoises are currently found on either of the major islands in Algoa Bay, following heavy rain on the mainland in 1981 an angulate tortoise, *Chersina angulata*, was found freshly dead on the shore of Bird Island (A. Batchelor, pers. comm.). It is possible that the two lizard species on St Croix Island in Algoa Bay could have been introduced to the island by rafting following floods in the rivers of the adjacent mainland. The spotted gecko *Pachydactylus maculatus* regularly shelters under bark on dead logs in the region (Branch, 1989), as does Tasman's girdled lizard *Cordylus tasmani*, a mainly arboreal cordylid endemic to the Algoa Basin (Branch and Braack, 1987). The Cape girdled lizard *Cordylus cordylus* is common among rocks along the Eastern Cape coast (Branch, 1988d).

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APPENDIX

Voucher specimens—AMNH, American Museum of Natural History, New York; CDNEC, Chief Directorate of Nature and Environmental Conservation, Jonkershoek; PEM R, Port Elizabeth Museum; SAM, South African Museum, Cape Town; TM, Transvaal Museum, Pretoria.

AMPHIBIA.

Breviceps rosei: **Robben Island**. SAM 2147, 2149, 2154, no date, Rev. G. H. R. Fisk. *Strongylopus grayii*: **Robben Island**. Poynton (1964) lists specimens from the Albany Museum, Grahamstown but these are unlocated.

REPTILIA.

Serpentes.

Colubridae. *Pseudaspis cana*: **Robben Island**. SAM 1725, 1882, H. W. Oakley; SAM 1847, no date, Sir R. Southey. *Lamprophis inornatus*: **Robben Island**. SAM 3528, 31 January 1899, D. Denyssen. (?) *Lycodonomorphus rufulus*: **Robben Island**. SAM 1857, no date, Rev. G. H. R. Fisk.

Elapidae. *Aspidelaps lubricus infuscatus*: **Pomono Island**. AMNH 51836, October 1925, H. Lang.

Sauria.

Gekkonidae. *Pachydactylus geitje*: **Robben Island**. SAM 157–158, 7 March 1881, H. W. Oakley; SAM 2049, December 1896, W. F. Purnell; SAM 43947–65, 10 June, G. R. McLachlan and U. van der Heever; TM 3575, 32791. *Pachydactylus maculatus*: **St Croix Island**. PEM R 239, 245, 250–52, 254, 262, 264; J. Spence, 8 October 1963. *Phyllodactylus porphyreus*: **Robben Island**. SAM 43979–80, 10 June 1976, G. R. McLachlan and U. van der Heever. **Jutten Island**. 9431–32, no date, Government Guano Department; SAM 44827–29, 4 November 1979, R. Brooke. **Dassen Island**. SAM 44830, 4 November 1979, R. Brooke; SAM 44833–34, 7 November 1979, R. Brooke; PEM R 4607–4623. **Meeuw Island**. SAM 44770–71, 27 April 1979, R. Brooke. **Marcus Island**. SAM 44776–77, 27 April 1979, R. Brooke. **Malgas Island**. TM 26162, 25 January 1951, Swedish Southern Africa Expedition. **Schaapen Island**. PEM R 1572–73, 1575–78, 1580, 1588–89, 18 April 1965, J. Spence and G. McLachlan. *Phyllodactylus lineatus*: **Schaapen Island**. SAM 44765–68, 27 April 1979, R. Brooke. **Meeuw Island**. SAM 44772–75, 27 April 1979, R. Brooke.

Chamaeleonidae. *Bradypodion pumilum*: **Robben Island**. FitzSimons (1943) records specimens in the Albany Museum but these are unlocated.

Agamidae. (?)*Agama atra*: **Dassen Island**. SAM 2644, April 1897, R. M. Lightfoot.

Scincidae. *Mabuya homalocephala*: **Robben Island**. SAM 1090–91, 1881, H. W. Oakley; SAM 1420–1446, 17 March 1881, H. W. Oakley. *Mabuya capensis*: **Dyer Island**. SAM 44836, 16 June 1979, R. Brooke. **Robben Island**. CDNEC 5612–13. *Scelotes gronovii*: **Meeuw Island**. SAM 44769, 27 April 1979, R. Brooke. **Schaapen Island**. SAM 43240, 4 May 1961, C. Gow; SAM 44764, 27 April 1979, R. Brooke; PEM R 554, 556–57, 561–64, 566–68, 18 April 1965, J. Spence and G. McLachlan. **Robben Island.** TM 35741, 16 May 1968, Dr J. M. J. Meier. **Dassen Island**. SAM 44835, 7 November 1979, R. Brooke; SAM 44831–32, 4 November 1979, R. Brooke; PEM R 4624–4632, 4566–67, TM 65844, 4–10 April 1987, W. R. Branch. PEM R 4633–4634, born in captivity to previous specimens. *Scelotes bipes*: **Robben Island**. SAM 1458–59, 1881, H. W. Oakley; SAM 1524–25, 1882, H. W. Oakley; SAM 1982–88, 21 April 1897, Dr Spencer; SAM 2025, 2027–29, 2031–40, 2042–43, no date, H. W. Oakley; SAM 2050, December 1896, R. M. Lightfoot. *Acontias meleagris meleagris*: **Schaapen Island**. SAM 44538, 2 May 1954, University of Cape Town Ecology Survey; PEM R 2007, 2010–11, 18 April 1965, J. Spence and G. McLachlan. **Robben Island**. SAM 1454–57, 1881, H. W. Oakley; SAM 2026, 2030, 2041, 2051, no date, H. W. Oakley; SAM 43937–46, 10 June 1976, G. R. McLachlan and U. van der Heever.

Cordylidae. **Cordylus cordylus**: **Jutten Island**. SAM 9430, no date, Government Guano Department; SAM 44825–26, 4 November 1979, R. Brooke. **Robben Island**. SAM 1104–06, 1880, R. Southey; SAM 2048, December 1896, W. F. Purnell; SAM 43932–36, 10 June 1976, G. R. McLachlan and U. van der Heever. **St Croix Island**. PEM R 521, J. Spence, 8 October 1963; R 1358–59, W. R. Branch, 7 July 1979. *Tetradactylus seps*: **Robben Island**. SAM 164–165, 1881, H. W. Oakley; SAM 1086–87, 1880, R. Southey; SAM 1187–1193, 7 March 1881, H. W. Oakley; SAM 1396–1419, 17 March 1881, H. W. Oakley.

Chelonii

Eretmochelys imbricata: **Dyer Island**. SAM 9403 (shell), 2 February 1906, H. Jackson, Government Guano Department.

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A revision of the tripterygiid fish genus *Norfolkia* Fowler, 1953 (Perciformes: Blennioidei)

by

W. HOLLEMAN

(Albany Museum, Grahamstown)

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ABSTRACT

The genus *Norfolkia* is revised and three species are recognised: *N. brachylepis* (Schultz) (= *N. springeri* Clarke) which is widespread throughout the tropical Indo-west Pacific, *N. squamiceps* (McCulloch and Waite) from the southern Barrier Reef, Norfolk and Lord Howe islands and *N. thomasi* Whitley from the Barrier Reef and south-central Pacific.

INTRODUCTION

Much tripterygiid taxonomy has advanced in a rather haphazard fashion, work tending to be regional. The first major generic revision was that of *Helcogramma* by Hansen (1986). Other genera now revised include *Tripterygion* by Wirtz (1980) and *Gilloblennius*, *Notochinops* and *Forsterygion* by Hardy (1986, 1987a, 1989). One of the problems that has beset tripterygiid taxonomy is the recognition of characters that adequately define genera (see Hardy, 1987a, b).

Most of the 14 genera listed by Hansen (1986) and including *Cremnochorites* (Holleman, 1982), *Karalepis* (Hardy, 1984), *Ceratobregma* (Holleman, 1987), *Bellapiscis* and *Cryptichthys* (Hardy, 1987b) can be defined by a combination of "stable" characters viz. the number of first dorsal fin and and anal fin spines, the number of pelvic fin rays and the configuration of the

lateral line. Combinations of these four characters do not hold stable for all genera and in *Forsterygion* and *Obliquichthys* (Hardy, 1987c) number of first dorsal fin spines, and in *Gilloblennius* and *Lepidoblennius* number of anal fin spines vary.

Members of the genus *Norfolkia* are medium-sized (max. 60 mm SL) tripterygiid fishes, widespread though not abundant throughout the Indian and western Pacific Oceans. One species is also known from the islands of the south-central Pacific. They are known only from tropical and subtropical waters occurring as far south as Cockburn Sound on the Australian west coast, where the mean winter (July to October) sea surface temperature is 18 °C. All species seem to be associated with coral or rocky reefs.

The colour pattern in preservative of the three species in the genus is rather similar with head and fins variously speckled with melanophores and the body carrying a number of irregular dark vertical bars. Colour photographs taken by R. Winterbottom and J. R. Allen and colour illustrations done by Patricia Hansen show marked differences in live colours.

Kuiter (1986) included in *Norfolkia* three species with three first dorsal fin spines, whereas *Norfolkia* was originally described with four first dorsal fin spines. There are, however, other osteological characters shared by the "four-spined" species not shared by Kuiter's "three-spined" species that preclude their inclusion in the genus. The purpose of this paper is to clarify which species belong in *Norfolkia* as well as to provide an adequate definition of the genus.

All measurements were taken as in Hubbs and Lagler (1958). Fin element counts follow Rosenblatt (1960) and Springer (1968). Snout profile (= snout angle) was measured as described in Holleman (1982). The method of counting vertebrae follows Hardy (1986, 1987a, b, c) who considers the first vertebra with a well developed, unforked haemal spine as the first caudal vertebra. Comparative morphometric data for the species are shown in Fig.1 and Table 1.

The following acronyms are used:

AMS – Australian Museum, Sydney
BPBM – Bernice P Bishop Museum, Honolulu
CAS – California Academy of Sciences, San Francisco
LACM – Natural History Museum of Los Angeles County
ROM – Royal Ontario Museum, Toronto
RUSI – JLB Smith Institute of Ichthyology, Grahamstown
USNM – United States National Museum, Smithsonian Institution
WAM – Western Australian Museum.

TAXONOMY

Genus *Norfolkia* Fowler, 1953

Norfolkia Fowler 1953:262. Type species *N. lairdi* Fowler 1953 = *Gillias squamiceps* McCulloch and Waite 1916:449, by original designation.

Diagnosis

First dorsal fin with four spines; anal fin with two spines; pelvic fin with two long rays united by a membrane for less than a quarter of their length or not at all; lateral line discontinuous, anterior series of pored scales ending below second dorsal fin and posterior series of notched scales from below end of anterior series to base of caudal fin. Orbital and anterior nasal tentacles present.

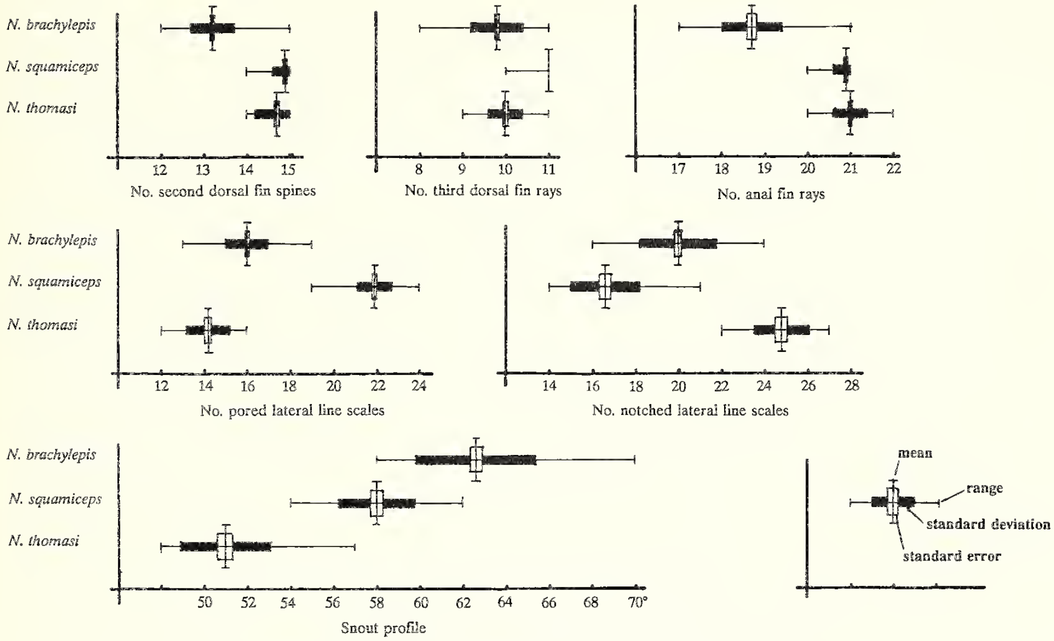

Fig.1. Selected meristic and morphometric data for the three species of *Norfolkia*.

Body and head behind and below eyes heavily scaled; scales ctenoid except for a few cycloid scales on pelvic fin bases, abdomen and around vent.

Margins of lateral ethmoids and frontals "crenulate". Septal bone (sensu Springer and Freihofer, 1976) unossified to partially ossified; vomer with single row of teeth; palatines edentate. First dorsal fin proximal pterygiophores in front of first vertebra. One or no free pterygiophore between second and third dorsal fins; caudal skeleton with two epurals and a substantial hypural 5; short broad neural spine on second pre-ural (penultimate) vertebra.

Description

Small fishes with fusiform bodies and pointed snouts; maximum recorded standard length 57 mm. First dorsal fin with 4 spines, second with 12–15 spines, third with 8–11 undivided segmented rays, except the last which is divided to its base. Anal fin with 2 short spines, the first supported by its own pterygiophore, the second sharing a pterygiophore with first of 17–21 undivided segmented rays; the last ray also always divided to its base. Last dorsal and anal fin rays supported by a pterygiophore and stay (Fig.2). Pelvic fins with one short hidden spine and two undivided segmented rays connected by a membrane for part of their length. Pectoral fins with 14–16 rays, the upper 2 or 3 undivided, the lower 7 undivided and thickened, remainder bifurcate. Caudal fin with 7 + 6 principal rays, uppermost and lowermost one or two undivided, remainder divided once; 6–7 dorsal and 4–6 ventral undivided procurrent rays.

Body, head behind eyes, cheeks to lower margin of eye and pectoral fin bases covered with ctenoid scales. Ctenii large and even-sized, posterior margins of scales slightly raised. Scales on abdomen and around vent smaller and cycloid.

TABLE 1. Fin and lateral line counts of *Norfolkia* species

		DORSAL 2 SPINES					DORSAL 3 RAYS				ANAL RAYS						
	No.	12	13	14	15	16	8	9	10	11	17	18	19	20	21	22	12
Norfolkia brachylepis																	
Natal	43		33	10				5	37	1		8	35				
Ceylon	5		5						5			1	4				
Christmas Island	5		5					1	4				5				
Taiwan	53	3	45	4	1		1	40	12		2	34	16				
Western Australia	38		30	8				1	28	7		2	29	7			
Philippines	6		5	1					6				6				
Queensland & NSW	21		6	14	1			1	20				6	13			
Norfolkia squamiceps																	
Lord Howe Island	10			2	8				1	9				1	9		
Norfolk Island	12			2	10					12				1	11		
Queensland																	
Heron Island	11				11					11					11		
One Tree Island	12				12					12				2	10		
Norfolkia thomasi																	
South Central Pacific																	
Rarotonga	2			1	2				2						2		
Rapa	3			1	2				3						3		
Western Pacific																	
Fiji	10			1	9				9	1					10		
One Tree Island	3				3				3						3		
Lizard Island	10			3	7				10					1	7	2	1
Heron Island	7			3	4			2	4	1				1	5	1	

	PORED LATERAL LINE SCALES												NOTCHED LATERAL LINE SCALES													
	13	14	15	16	17	18	19	20	21	22	23	24	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Norfolkia brachylepis																										
Natal			1	9	16	1											1	1	1	2	10	2	1			
Ceylon				3	1												1		1	2						
Christmas Island				2	3														2		1					
Taiwan		4	3	16	18	1									1	2	9	12	1		2					
Western Australia				9	10	6	1										6	2	2	4						
Philippines				3															1		1					
Queensland & NSW			2	7	6														4	2	4	1				
Norfolkia squamiceps																										
Lord Howe Island									2	3	1				3		1									
Norfolk Island										4	4	1	2	2	1											
Queensland																										
Heron Island									5	6				1	5	3	1	1		1						
One Tree Island															1	2	1									
Norfolkia thomasi																										
South Central Pacific																										
Rarotonga			1	1																	1				1	
Rapa		1		1																						
Western Pacific																										
Fiji	2	1	1																					1		1
One Tree Island																										
Lizard Island	3	1	1																					1	1	
Heron Island		3	2																				3	1	1	

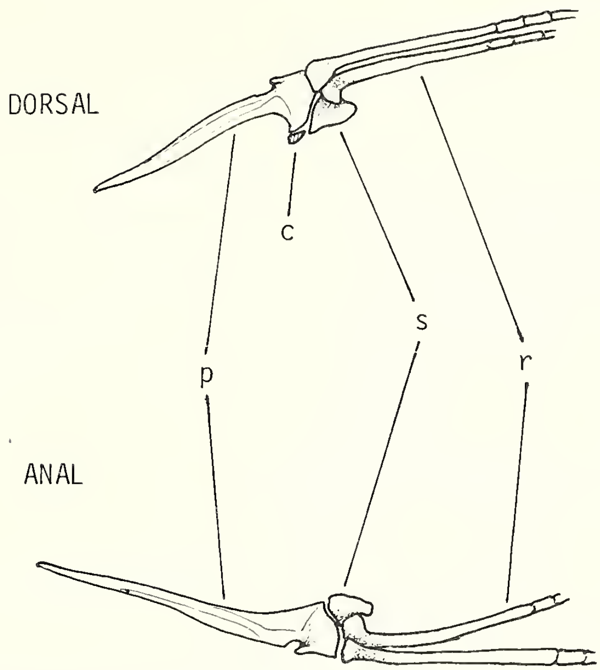

Fig. 2. Last dorsal and anal fin elements of *N. squamiceps*. p - distal pterygiophore; s - stay; r - divided ray; c - cartilage.

Anterior lateral line series with 12–24 pored scales extending as far as the junction of the second and third dorsal fins; posterior series with 14–27 notched scales running from three scale rows below end of anterior series to base of caudal fin. Orbital and anterior nasal tentacles present. Teeth in jaws and on vomer conical and fixed; palatines edentate. Septal bone unossified to partially ossified. Margins of lateral ethmoids and frontals "crenulate" to greater or lesser degree (Fig.3). Posterodorsal margin of post-temporal bone serrate. One or two spines lost from second dorsal fin, resulting in no or one free pterygiophore between second and third dorsal fins. Precaudal vertebrae 10 or 11 (rarely 12), caudal vertebrae 24–27. Caudal skeleton with two epurals, a large hypural 5 and a short neural spine on the pre-ural centrum.

Discussion

There are only two tripterygiid genera with four first dorsal fin spines, two anal fin spines and a discontinuous lateral line: *Norfolkia* and *Cremnochorites*. These two genera were shown to be clearly distinct by Holleman (1982). *Norfolkia* spp. lack the denticle-like head scales, palatine teeth and completely ossified septal bone of *Cremnochorites*. In *Norfolkia* the septal is usually unossified but some cleared and stained specimens of *N. brachylepis* and *N. squamiceps* show partial ossification, starting from the posterior margin. The cephalic lateralis canals of *Cremnochorites* are closed (the bone forms a 'tube' with pores), whereas those of *Norfolkia* are open (the bone is an open channel).

The crenulate margins of the lateral ethmoids are curious, giving the impression that the bone has been eroded away, leaving irregular remnants of bone embedded in the tissue (Fig.3a).

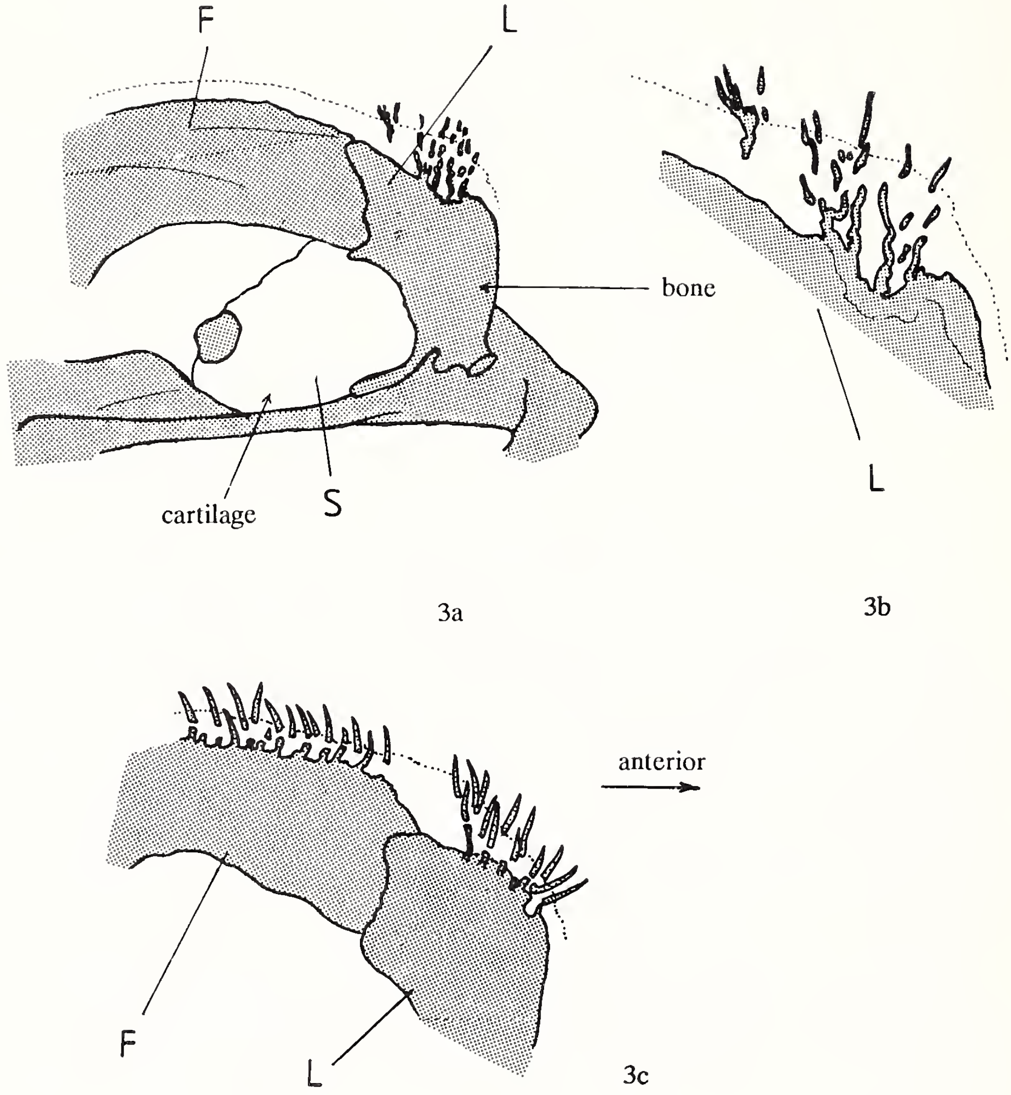

Fig. 3.a: Lateral view of anterior of cranium *N. brachylepis* showing "crenulate" margin of lateral ethmoid and partially ossified septal. b: enlarged portion of lateral ethmoid margin shown in 3a. c: portion of lateral ethmoid and frontal of *N. squamiceps*. f–frontal; l–lateral ethmoid; s–septal.

Sometimes the remnants resemble thin spines, parallel sided and pointed, the tips protruding through the skin (Fig.3b). The orbital margin of the frontals has similar "crenulations" or "spines".

This character is autapomorphic for *Norfolkia*, it not having been observed in any other tripterygiid species, or in any other blennioid fish. *Norfolkia* shares with *Cremnochorites*, *Forsterygion* and *Apopterygion* Kuiter a serrated posterodorsal margin on the post-temporal (Hardy, 1989). This serrated margin is also present in "*Norfolkia*" *clarkei* (= *Tripterygion striaticeps*, see Kuiter, 1986). Hardy (1989) suggested—and this author concurs—that the phylogenic significance of this character is unclear and it may well have been independently derived by these four genera (and whatever genus "*N*". *clarkei* is referable to).

Only three species are here recognised: *Norfolkia brachylepis* (Schultz), *N. squamiceps* (McCulloch and Waite) and *N. thomasi* Whitley. The three species included by Kuiter (1986) in *Norfolkia* have only three spines in the first dorsal fin and lack the distinctive "crènulate" margins of the lateral ethmoids and frontal bones. They are consequently not referable to the genus.

The distribution of the three recognised species of *Norfolkia* is shown in Fig.4.

Key to the species of *Norfolkia*

1 (a) Second dorsal fin spines 15 (rarely 14); anal fin rays 21 2
(b) Second dorsal fin spines 12–15, usually 13; anal fin rays 18–20 .... *N. brachylepis*
2 (a) Third dorsal fin rays 11; pored scales in anterior lateral line series 21–24 .... *N. squamiceps*
(b) Third dorsal fin rays 10, rarely 9 or 11; pored scales in anterior lateral line series 12–15 .... *N. thomasi*

Norfolkia brachylepis (Schultz) (Fig.5)

Tripterygion brachylepis Schultz 1960:291, type locality, Bikini Atoll, Marshall Islands.
Norfolkia springeri Clark 1979:95, type locality Gulf of Elat, Red Sea.

Description

Dorsal fins IV + XII-XV + 9–11, usually IV + XIII + 10 (except for specimens from southern western Australia and New South Wales—see below); first dorsal fin lower than second. Anal fin II + 18–20, usually II + 19 rays; pectoral fins 15 or 16, usually 16 rays, upper 2 simple, lower 7 simple and thickened, remainder divided once. Caudal fin with 5–7 dorsal, 5 ventral procurrent rays. Pelvic fin rays not united by a membrane. Lateral line anterior series 14–18, usually 16–17 pored scales, ending below last 3 spines of second dorsal fin; posterior series of 18–23 notched scales from third scale below end of anterior series, overlapping it by 1–2 scales, to base of caudal fin. Transverse scales 3/8; total lateral scales 31–34, usually 32 or 33.

Precaudal vertebrae 11 (rarely 12), caudal vertebrae 24 rarely 23 (as a result of fusion of PU2 and PU3) or 25. Pleural ribs 7, epipleural ribs 11; no intramuscular bones. One or two dorsal fin spines lost, leaving no or one free pterygiophore between second and third dorsal fins.

Head profile slightly rounded, interorbital area concave. Nasal bone not bridged or narrowly bridged. Orbital and nasal tentacles finely serrated. Scales on head extend to below lower margin of eye. Pectoral fin bases heavily scaled; abdominal scales cylcoid, extending to base of pelvic fins. Mandibular pores 4 + 1 + 4 (Fig.6). Head 3,0–3,7 in SL; eye 2,9–3,8 in head; upper jaw 2,1–2,8 in head; snout 3,3–4,7 in head; snout profile 58°–70°.

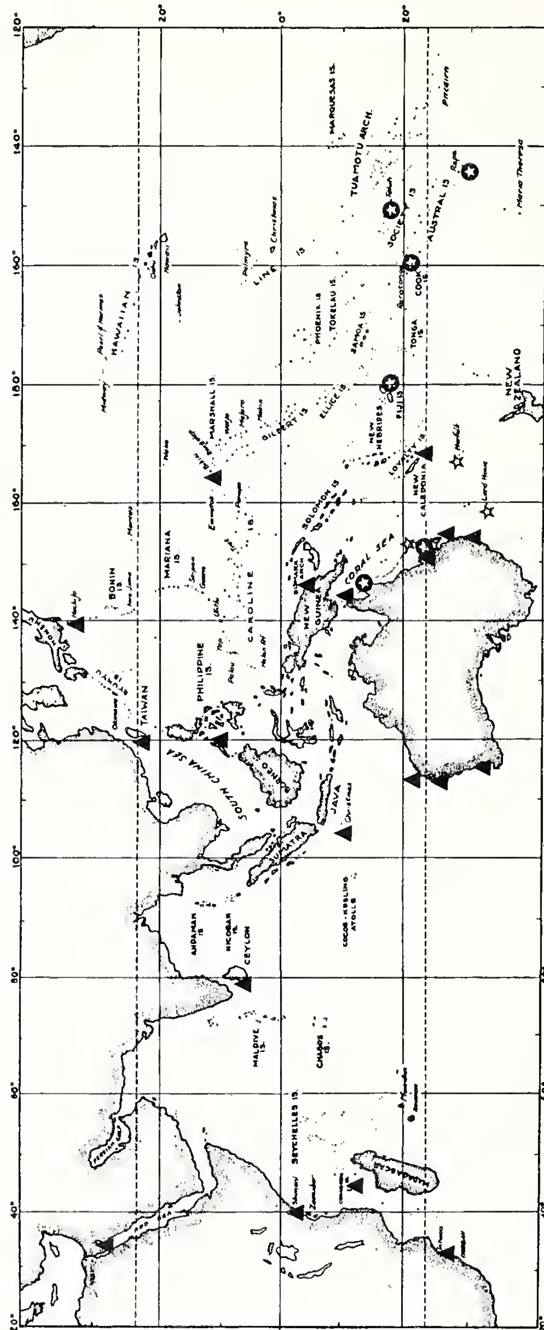

Fig. 4. Distribution of the genus *Norfolkia*. ▲ *N. brachylepis* ☆ *N. squamiceps* ✪ *N. thomasi*

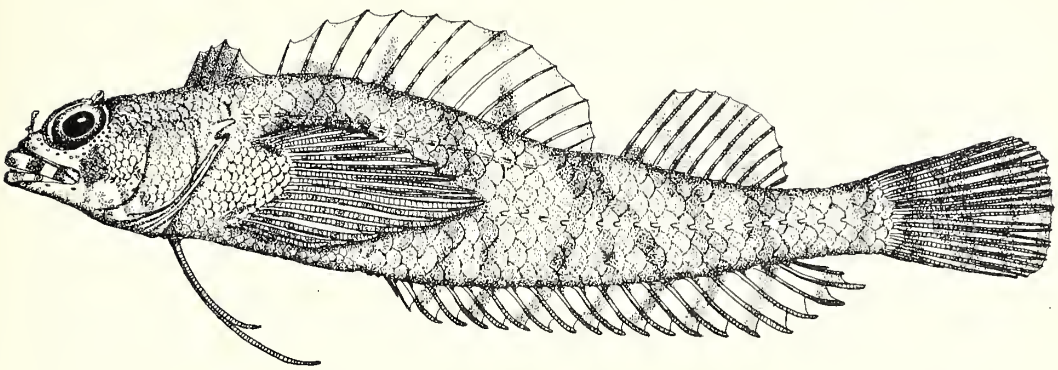

Fig. 5. *Norfolkia brachylepis*, female, 35.0mm SL, from AMS I20770-012.

COLOUR

In preserved specimens there are six dark bars running diagonally from the dorsum to the midline below which they divide to form a series of 10 or more squarish blocks. Anal fin is distinctly barred, the bars running diagonally forward from the base of the fin. Caudal fin with broad dark bars, leaving narrow clear bands between the bars. Pectoral fins spotted, dorsal fins dusky. Head unevenly covered with melanophores with a relatively distinct bar running from below mid-eye to behind corner of the mouth.

Patricia Hansen made a colour painting of freshly dead material from Japan in 1978, which shows the second and third dorsal fins suffused with deep red, the body a light brown. Colour photographs of *N. brachylepis* published by Allen (1985:2447) show a mottled orange head, a light brown flecked body with chocolate-brown bars with red flecks and reddish brown bars on the second and third dorsal fins. (Allen's Plates 415 and 416 are possibly male and female of the same species.)

Comparisons

Norfolkia brachylepis can easily be distinguished from the other two *Norfolkia* species by generally lower counts of second and third dorsal and anal fins (see Fig.1 and Table 1) and by the distinctly banded anal fin. Some specimens of both *N. thomasi* and *N. squamiceps* do show light and irregular banding on the anal fin.

Distribution

In a revision of the South African Tripterygiidae (Holleman, 1978) *Norfolkia* specimens from Natal were found to be conspecific with *N. springeri* described from the Red Sea by Clark (1979). This was confirmed when the author saw the types of *N. springeri* at the National Museum of Natural History in 1979. This study shows that the Natal material is conspecific with the material from the eastern Indian and Pacific Oceans. *N. springeri* is thus the junior synonym of *N. brachylepis*.

The distribution of *N. brachylepis* is far more extensive than that of either *N. squamiceps* or *N. thomasi* (Fig.4). Its habitat ranges from coral reefs in tropical waters to rocky reefs in warm temperate waters around Perth, Western Australia.

N. brachylepis also exhibits a greater variation in the number of dorsal and anal fin elements than do the other two species. Where there are 13 second dorsal fin rays there is one free pterygiophore between second and third dorsal fins; where there are 14 there is no free pterygiophore. The most common combination is 13 second dorsal fin spines, 10 third dorsal fin rays and 19 anal fin rays. The last dorsal ray is always associated with the 8th last vertebra and the last anal fin ray with the 7th last vertebra.

Norfolkia squamiceps (McCulloch and Waite) (Fig.7)

Gillias squamiceps McCulloch and Waite 1916: 449 (original description, based on three specimens from Lord Howe Island).

Norfolkia lairdi Fowler 1953: 264 (type species of the genus, based on one (?) specimen from Norfolk Island).

Description

Dorsal fins IV + XIV-XV + 10–11, usually IV + XV + 11; first dorsal fin lower than second. Anal fin II + 20–21 rays, usually 21; pectoral fin 16 rays, upper 2–3 simple, lower 7

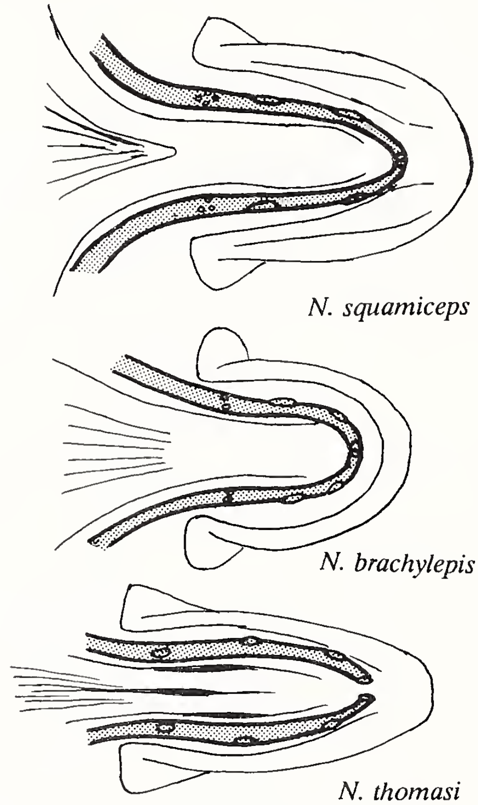

Fig. 6. Mandibular pore patterns of the three species of *Norfolkia*.

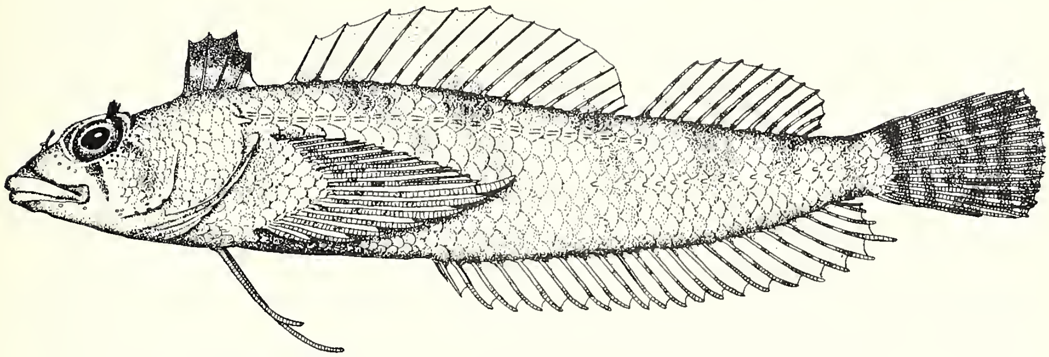

Fig. 7. *Norfolkia squamiceps*, female, 57,5mm SL, from AMS I17368-019.

simple and thickened, remainder bifurcate. Caudal fin with 6 or 7 dorsal and 5 or 6 ventral procurrent rays; pelvic fin rays united by membrane for less than one quarter of the length of the short ray; lateral line anterior series 21–24, usually 22, pored scales, ending below the junction of the second and third dorsal fins; posterior series 14–19, usually 16, notched scales, third scale row below anterior series, from end of anterior series which it may overlap by as many as 4 scales, to base of caudal fin. Transverse scales 4/8; lateral scales 32–35, usually 34.

Precaudal vertebrae 11, caudal vertebrae 24–26, usually 25. Pleural ribs 9, epipleural ribs 14, 3 intramuscular bones. One dorsal fin spine lost, no free pterygiophore between second and third dorsal fins.

Interorbital concave. Nasal bones long and narrow and narrowly bridged. Palmate nasal and orbital tentacles present; margins of orbits with many small spines and margins of lateral ethmoid and frontal bones heavily "crenulate". Opercles and pectoral fin bases heavily scaled with ctenoid scales; abdomen with cycloid scales extending to base of pelvic fins. Mandibular pores 5–6 + 1 + 5–6 (Fig.6). Head 2,9–3,6 in SL; eye 3,0–3,9 in head, upper jaw 2,3–3,0 in head, snout 3,3–4,9 in head. Snout profile 54°–62°, mean 58°.

Colour

No live or freshly caught specimens have been seen. In preservative all *Norfolkia* species show remarkably similar pattern of body and fin markings and bars below the eyes.

Light coloured specimens of *N. squamiceps* show five irregular dark bars along back which fade toward the midline and disappear below it. All fins except the pelvics have narrow irregular bars (these are often absent on the anal fin); first dorsal fin usually darker than others, may lack the barring except on first spine. There is a short, dark bar below and one behind the eye on the preopercle. The orbital tentacles are dark. In small specimens pigmentation is more intense and patterning clearer. In dark specimens body bars become obliterated by an even scatter of melanophores over the body and head. The dorsal fins are very dark; anal fin very dark, without any barring, and with the margin unpigmented; caudal and pectoral fins retain light, irregular bars; pelvic fins remain unpigmented. Head is darker but retains bars below and behind eyes.

There appears to be no sexual dichromatism but it is reasonable to presume that the males, like those of many other tripterygiids, will show darker breeding coloration.

Comparisons

N. squamiceps can be distinguished from *N. thomasi* by its longer anterior lateral-line series (22 vs 13 pored scales) and concomitantly shorter posterior series of notched scales (16 vs 25), scales on head which extend to below the eyes and cover the opercula, and a blunter snout (58° vs 51°). The species can be distinguished from *N. brachylepis* by higher dorsal and anal fin counts.

Distribution

N. squamiceps appears to have a limited distribution range (Fig.4). It was described from specimens from Lord Howe and Norfolk Islands. Subsequent material has been collected at these two islands, the Swain Reefs and One Tree and Heron islands, southern Queensland.

***Norfolkia thomasi* Whitley** (Fig.8)

Norfolkia thomasi Whitley 1964: 192.

Description

Dorsal fins IV + XIV-XV + 9–11, usually IV + XV + 10; first dorsal fin lower than second. Anal fin II + 20–22, usually 21; pectoral fin 14–16, usually 15 rays; upper 1–2 simple, lower 6–7 simple and thickened, remainder bifurcate. Caudal fin with 6 dorsal and 5 ventral procurrent rays; pelvic fin rays not united by membrane. Lateral line anterior series 12–15, usually 14, pored scales, ending below spines 9–11 of second dorsal fin; posterior series 24–27, usually 25 notched scales, from third scale row below anterior series, overlapping it by 0–1 scales, to base of caudal fin; transverse scales 3/8 lateral scales 34–36, usually 35. Precaudal vertebrae 11, caudal vertebrae 26. Pleural ribs 4, epipleural ribs 7, intramuscular bones 3. Two dorsal fin spines lost leaving one free pterygiophore between second and third dorsal fins.

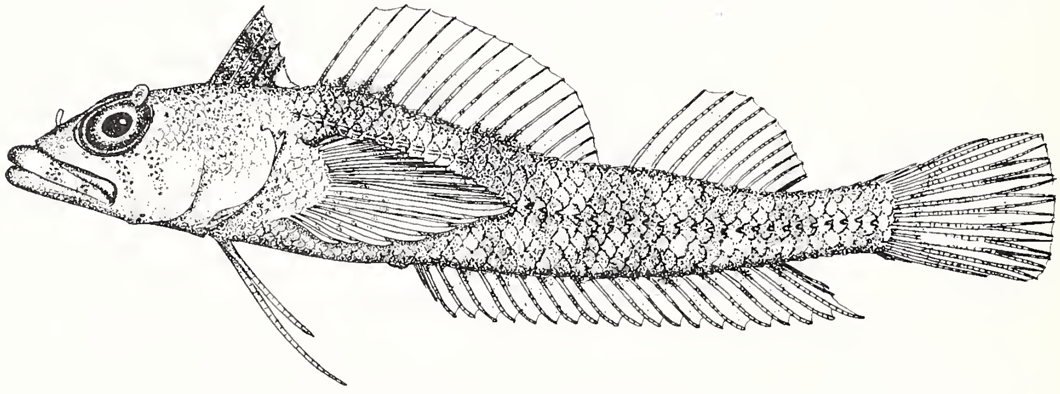

Fig. 8. *Norfolkia thomasi*, male, 30,0mm SL, from USNM 238854.

Head flattened, snout long and sharp. Fine "toothing" on margin of frontals and lateral ethmoids. Interorbital flat to slightly concave, with ascending processes of premaxillae extending well beyond midpoint of upper margin of eyes. Large lobate orbital and anterior nasal tentacles present. Scales on head extend only to lower margin of eye; pectoral fin bases scaled; abdominal scales cycloid, extending to base of pelvic fins. Mandibular pores 3 + 2 + 3 (Fig.6). Head 2,9–3,2 in SL; eye 3,5–4,9 in head, upper jaw 2,1–2,5 in head, snout 3,0–4,2 in head. Snout profile 48°–57°, mean 51°.

COLOUR

No live or freshly dead specimens have been seen. There are six more or less distinct dark bars running diagonally back from the dorsum on to the midline. Below the midline they tend to coalesce and fade. In small specimens markings are more distinct and below midline a number of irregular, narrow bands are formed. A series of dark spots at base of anal fin extend as light banding on fin. Other fins irregularly banded except for first dorsal fin which is dark. Head evenly dusted with melanophores except for single darker band extending from lower margin of eye diagonally backwards over preopercle. Orbital tentacle dark.

No sexual dichromatism apparent.

Comparisons

See under *N. squamiceps*.

Distribution

N. thomasi is known from the southern Queensland (Heron and One Tree islands), Lizard Island in the north of the Barrier Reef (and thus presumably in between) from the Fiji Islands, and from the Cook (Rarotongla), Society (Tahiti) and Rapa (Rapa Iti) islands (Fig.4). In the light of Springer's (1982) work on shore fish distribution, this species' distribution across the western margin of the Pacific plate to the Cook, Society and Rapa islands is unexpected. There is, however, no reason to consider the specimens from these islands to be of a different species. It is not known whether *N. thomasi* occurs in New Caledonia or the New Hebrides, respectively marginally off and marginally on the Pacific Plate.

ACKNOWLEDGEMENTS

The author is grateful to the institutions listed in the introduction for the loan of material for a very protracted time, particularly to Doug Hoese, the Australian Museum, Jerry Allen, Western Australian Museum, Rick Winterbottom, Royal Ontario Museum and Jack Randall, B P Bishop Museum. Particular thanks go to Phil Heemstra for useful comments on the manuscript.

MATERIAL EXAMINED

Norfolkia brachylepis

Western Indian Ocean
BPBM XXXXX (7, 27,0–43,0); Sodwana Bay, Zululand, Natal.
RUSI 8703 (7, 30,4–40,0); Sodwana Bay, Zululand, Natal.
RUSI 8704 (2, 31,4 & 40,3); Sodwana Bay, Zululand, Natal.
RUSI 8705 (2, 38,8 & 44,5); Boteler Point, Zululand, Natal.

RUSI 8706 (5, 28,9–32,7); Sodwana Bay, Zululand, Natal.
RUSI 8707 (5, 27,9–41,0); Sodwana Bay, Zululand, Natal.
RUSI 8708 (16,8); Sodwana Bay, Zululand.
RUSI 8709 (2, 27,6 & 31,1); Sodwana Bay, Zululand, Natal.
RUSI 8710 (6, 19,7–40,8); Hulley Point, Zululand, Natal.
RUSI XXXXX (32,6); Inhaca Island, Mozambique.
RUSI 7386 (34,0); Shimoni, Kenya.
USNM 231788 (2, 33,0); Anjouan Island, Comoro Islands.

Central Indian Ocean
USNM 231789 (37,8); Trincomalee, Ceylon.
USNM 231787 (22,9); Fort Frederick, Trincomalee, Ceylon.
USNM 231783 (23,0); Kaddukulam Pattu, Trincomalee, Ceylon.
USNM 231765 (3,20,7–40,0); Fort Frederick, Trincomalee, Ceylon.
USNM 231758 (2,18,5 & 21,5); Trincomalee, Ceylon.

Eastern Indian Ocean
WAM P26610–016 (2, 29,8 & 30,3); Smith Point, Christmas Island.
WAM P26122–012 (3, 27,9–31,2); Nortwest Point, Christmas Island.
WAM P26656–001 (43,7); Shark Bay, Western Australia.
WAM P26657–016 (2, 36,3 & 38,5); Shark Bay, Western Australia. WAM P26664–009 (42,6); Shark Bay, Western Australia.
WAM P26670–014 (6, 17,0–46,8); Dirk Hartog Island, Western Australia.
WAM P26662–014 (4, 37,6–47,0); Shark Bay, Western Australia.
WAM P27616–032 (2, 33,1 & 37,6); Rottnest Island Western Australia.
WAM P25374–012 (14, 27,4–46,3); nr. Tantabiddi Creek, North west Cape.
WAM PXXXXX-XXX (6, 33,3–42,2); Garden Island, nr Perth, Western Australia.
WAM P26671–016 (3, 37,2–47,2); Shark Bay, Western Australia.
AMS I20229–038 (38,5); Carnac Island, Cockburn Sound, Western Australia.

Western Pacific Ocean
USNM 227496 (29,5); nr. Ch'uan-fan-shih, Taiwan.
USNM 231769 (8, 20,0–35,5); nr. Ch'uan-fan-shih, Taiwan.
USNM 231763 (11, 17,3–42,3); Chin-chia-wan, Taiwan.
USNM 231773 (4, 27,2–32,5); Mao-Pi T'ou., Taiwan.
USNM 231762 (30,8); Ch'nan-fan-shih, Taiwan.
USNM 231770 (31,4); Ch'uan-fan-shih, Taiwan.
USNM 231781 (4, 18,2–37,5); Sha Toa, Taiwan.
USNM 231778 (31,5); nr Ch'uan-fan-shih, Taiwan.
USNM 231775 (12, 25,0–41,2); nr. Ch'uan-fan-shih, Taiwan.
USNM 231759 (2, 30,0 & 30,5); nr. Ch'uan-fan-shih, Taiwan.
USNM 231767 (13,2); Chin-chia-wan, Taiwan.
USNM 231760 (34,5); nr. southern tip of Taiwan.
USNM 231772 (3, 18,2–31,4); nr. southern tip of Taiwan.
USNM 231764 (4, 26,9–33,3); Ch'uan-fan-shih, Taiwan.
USNM 231790 (4, 19,9–34,2); Taganayan Island, Palawan, Philippine Islands.

USNM 231780 (34,0); nr. Maloh, Negros Oriental, Philippine Islands.
USNM 231792 (30,0); Cuyo Island, Palawan, Philippine Islands.
USNM 231791 (4, 24,2–30,5); Cuyo Island, Palawan, Philippine Islands.
USNM 231774 (44,5); Miyake Jima, Izu Islands, Japan.
USNM 231777 (19,2); Miyake Jima, Izu Islands, Japan.
USNM 231784 (24,3); Paeowai Island, Madang Harbour, Papua—New Guinea.
USNM 231768 (28,7); Mare, Loyalty Islands.
AMS I20756–010 (25,0); Great Detached Reef, Raine Island, Queensland.
AMS I20770–012 (3, 25,8–34,3); South Island, Sir Charles Hardy Island, Queensland.
ROM 38215 (32,5); Queensland.
WAM P27065–016 (6, 23,5–31,2); Bagara, Kelly's Beach, Queensland.
WAM P27075–018 (3, 34,5–42,8); Julian Rocks, Byron Bay, New South Wales.
WAM P27082–014 (3, 35,0–41,0); Solitary Island, New South Wales.
WAM P27076–020 (5, 27,9–41,3); Julian Rocks, Byron Bay, New South Wales.

Norfolkia squamiceps
AMS IA937 (38,5 mm SL); Lord Howe Island.
AMS IB3544 (40,7 mm SL); Heron Island, Queensland.
AMS IB6161 (41,8 mm SL); Gillett Cay, Swain Reefs, Queensland.
AMS I17368–019 (32, 18,9–57,0 mm SL); Lord Howe Island.
AMS I20205–053 (32,2 mm SL); One Tree Island, Queensland.
AMS I20270–014 (9, 25,6–43,0 mm SL); Philip Island, Norfolk Island.
AMS I20271–035 (3, 40,7–45,0 mm SL); Bumbora Beach, Sydney Bay, Norfolk Island.
AMS I 21451–003 (33,8 mm SL); One Tree Island, Queensland.
LACM 39986-37 (4, 19,5–35,0 mm SL); Heron Island, Queensland.
USNM 231782 (9, 19,4–39,0 mm SL); One Tree Island, Queensland.
USNM 231761 (3, 23,0–27,3 mm SL); Heron Island, Queensland.
USNM 231776 (3, 35,0–40,9 mm SL); Heron Island, Queensland.
USNM 231779 (5, 17,3–35,0 mm SL); One Tree Island, Queensland.

Norfolkia thomasi
Holotype—AMS IB 4020 (37,4 mm); Gillett Cay, Swain Reefs, Queensland. (Fowler (1953:193) gives the number as IB 4040)

Non-types: Queensland
AMS I 19108–105 (5:17,2–28,9 mm); Bird Islet, Lizard Island, Queensland.
AMS I 19338–026 (4:17,6–40,3 mm); One Tree Island, Queensland.
AMS I 20201–019 (5:14,0–35,0 mm); Heron Island, Queensland.
AMS I 20557–005 (2:18,0–212,2 mm); One Tree Island, Queensland.
AMS I 20774–013 (3:22,0–33,3 mm); Cape Melville, Queensland.
AMS I 21422–125 (2:35,1 & 35,5 mm); Lizard Island, Queensland.
AMS I 22634–011 (33,9 mm); Escape Reef North, Queensland.
LACM 39985-58 (4:34,1–37,4); Heron Island, Queensland.
USNM 231766 (36,2 mm); One Tree Island, Queensland.
USNM 231771 (40,5 mm); One Tree Island, Queensland.
USNM 231786 (42,0 mm); One Tree Island, Queensland.

WAM P 24735 (33,7 mm); Lizard Island, Queensland.

Western Pacific

ROM 56791 1 (26,5 mm); Dravuni, Astrolabe Reef, Fiji Islands.
ROM 56792 1 (27,0 mm); Dravuni, Astrolabe Reef, Fiji Islands.
ROM 56793 1 (25,2 mm); Vanuakula, Kadavu, Fiji Islands.
ROM 56794 1 (24,8 mm); Astrolabe Reef, Fiji Islands.
USNM 238852 (26,6 mm); Totoya Island, Fiji Islands.
USNM 238853 (33,7 mm); Navutu Ira Island.
USNM 238854 (2:24,5 & 30,1 mm); Malamala Island.
USNM 238855 (2:24,9 & 29,5 mm); Totoya Island, Fiji Islands.

South Central Pacific

BPBM 17196 (3:30,5–31,7 mm); Haurei Bay, Rapa Iti.
BPBM XXXXX (35,0 mm); Raratonga, Cook Islands.
CAS 38838 (32,3 mm); Tahiti.
ROM 38215 (32,3 mm); Rarotonga, Cook Islands.

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Some aspects of the ethology of five species of Eumenidae (Hymenoptera) in southern Africa.

by

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(Albany Museum, Grahamstown)

*(The order of names is alphabetical and joint authorship should be understood. The same applies to previous papers on the ethology of Hymenoptera by the same authors.)

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ABSTRACT

Ethological accounts are given for five eumenids, two excavating nests in horizontal ground, *Allepipona erythrospila* (Cameron), *Antepipona scutellaris* Giordani Soika, and three nesting in pre-existing cavities above ground, *Euodynerus euryspilus* (Cameron), *Rhynchium marginellum sabulosum* (Saussure), and *Tricarinodynerus guerinii* (Saussure). Associated insects, megachilid bees, chrysidids, bombyliids and meloids are noted.

INTRODUCTION

Gess (1981) published some aspects of an ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown. This paper was based on a survey of the aculeate wasps and bees of a farm Hilton, 18 kilometres WNW of Grahamstown (33° 19′S,

26° 32′E) in the Eastern Cape Province of South Africa. The location, topography, geology, climate and vegetation of the study area were outlined. An annotated list of 241 species arranged on the basis of their ethology was given. There followed a discussion of the nesting behaviour of the community as a whole showing how the diversity of the ethology of such a large number of sympatric species results in their ecological displacement and giving some indication of the phylogenetic pattern leading to this diversity.

Those species the ethology of which added significantly to the knowledge of the ethology of the genera or even families to which they belong were selected as the subjects for a series of papers published in the *Annals of the Cape Provincial Museums (nat. Hist.)* (1974–1988). There remains a considerable volume of fieldnotes on species the ethology of which is unknown or poorly known in published accounts but which, though adding to the knowledge of the genera and families to which they belong, offer nothing of particular note. The accounts of some aspects of the ethology of five eumenids, *Allepipona erythrospila* (Cameron), *Antepipona scutellaris* Giordani Soika, *Euodynerus euryspilus* (Cameron), *Rhynchium marginellum sabulosum* (Saussure), and *Tricarinodynerus guerinii* (Saussure), presented here are in this category. The justification for their publication is that this basic information is required as background to a project on nest parasites currently being undertaken by A. J. S. Weaving of the Albany Museum.

The order in which the species accounts are presented is alphabetical and does not imply relationships.

ETHOLOGICAL ACCOUNTS

Allepipona erythrospila (Cameron)

Geographic distribution

Allepipona erythrospila (Cameron) has been recorded from the Cape Province, the Orange Free State and Lesotho (Giordani Soika, 1987).

The farms Brak Kloof, one of the two type localities of *A. erythrospila*, and Hilton, the locality of the present study, adjoin one another.

Description of nesting sites

Two nests of *A. erythrospila* were investigated at Hilton. Both were situated in level areas of denuded clayey soil, one above and one below a furrow (Gess, 1981: Fig. 6), near (137 cm in one instance) the edge of shallow puddles resulting from recent rain.

Flight period

The flight period of *A. erythrospila* at Hilton, as deduced from twenty-three specimens collected, starts in October and continues into March. The two instances of observed nesting were on 20.xi.1973 and 27.iii.1974.

Flower visiting

The authors are aware of only one record of *A. erythrospila* visiting flowers: one female on the yellow flowers of *Berkheya heterophylla* (Thunb.) O. Hoffm. (Asteraceae), Strowan, Grahamstown, 12.x.1972, F. W. Gess.

Identification of prey and location of sting sites

The single prey obtained was a caterpillar of the family Pyralididae. It was olive-green with longitudinal paler stripes and pale setal warts, and was 18,3 mm in length.

Sting sites were present in the region of the neck and on the second abdominal segment.

Description of nest

One of the two nests of *A. erythrospila* consisted of a short burrow surmounted by a collar constructed from mud pellets and of the same inner diameter as the shaft. The collar was similar in appearance to that of *Parachilus insignis* (Saussure) though smaller in diameter.

The second nest, when discovered, lacked a collar. It appeared that there had probably been a collar which had been destroyed by the trampling of sheep. The burrow of this nest consisted of a short curved shaft slightly dilated at its lower end to form a cell. Provisioning was still in progress and so it is not known what the nature of the seals would have been.

Method of construction of nest, oviposition and provisioning

Water is required for burrow excavation. It is collected from a nearby pool and carried to the nest in the crop. When filling her crop, an activity commonly observed, a wasp stands on the mud at the edge of the water.

Observation of the second nest began at 11.30 am by which time a short burrow had already been excavated. Consequently initiation of the nest and construction of the turret were not observed but will almost certainly have followed a similar pattern to that described for *Parachilus insignis* (Gess and Gess, 1976).

Further pellets extracted from the burrow were discarded in a distinct pellet dropping area. This was situated on the far bank of the puddle at a distance of 190 cm from the nest. The wasp always left the nest in a fixed direction and returned from a fixed direction, the flight path to the pellet dropping area and back to the nest having been more or less constant and in the form of an ellipse.

In only one instance was the number of pellets formed with the aid of a single crop-full of water recorded. In that instance the number was nine.

During burrow excavation the wasp always entered head first (Fig. 1a and b) and exited backwards, bearing a pellet (Fig. 1c). At about 12.30 pm, an hour after the start of observations, the burrow and the cell at its end had been completed and the last pellet was carried away and dropped.

On returning from dropping this pellet the wasp alighted next to the nest entrance as usual but then turned around and backed down the burrow (Fig. 1d) in order to oviposit in the empty cell. The egg, 2,2 mm long and 0,68 mm wide at mid-length, was suspended from the ceiling of the cell by a filament about 0,6 mm long.

Oviposition having taken place provisioning commenced. The wasp emerged from the burrow (Fig. 1e) and flew off, returning after ten minutes with a long caterpillar held beneath her body by her mandibles and legs, the prey's head being directed forwards. On alighting next to

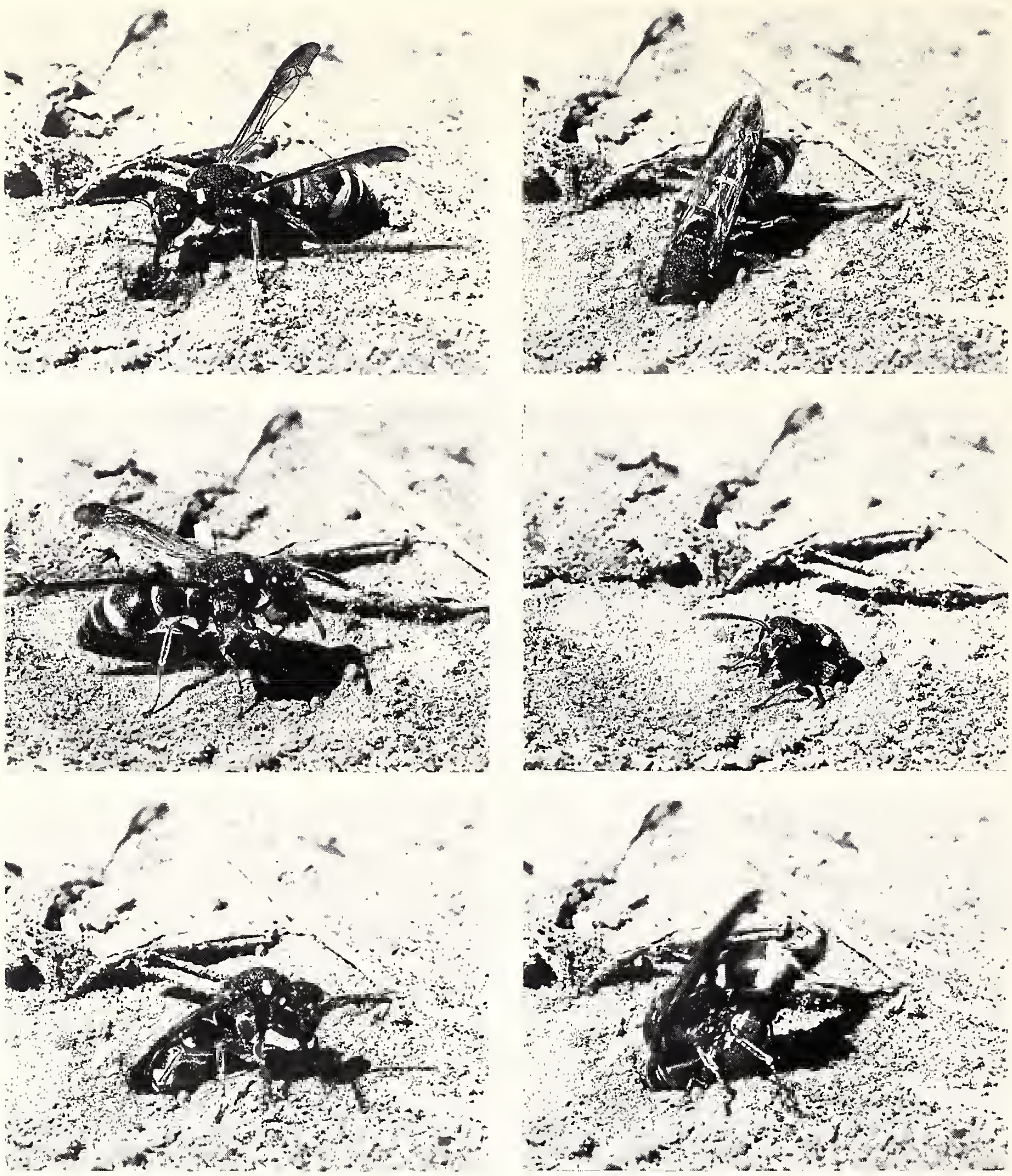

Fig. 1. *Allepipona erythrospila* (Cameron) , Hilton, 27.iii.1974: (a) about to enter nest under construction; (b) entering nest under construction; (c) About to fly off with mud pellet held between jaws; (d) Entering nest backwards in order to oviposit in cell; emerging from nest after ovipositing; (f) Entering nest with prey. (× *c* 2,5)

the nest entrance the wasp retained her hold of the prey with her mandibles and, with her legs straddling the prey, entered the burrow (Fig. 1 f).

The wasp was captured upon re-emerging from the nest which was then investigated. It is therefore not known whether any additional caterpillars would have been used to provision this cell or whether any further cells would have been constructed.

Antepipona scutellaris Giordani Soika

Geographic distribution

Antepipona scutellaris Giordani Soika has to date been recorded only from the Cape Province (Giordani Soika, 1985).

The farm Hilton, the locality of the present study, is one of the type localities of *A. scutellaris*.

Description of nesting sites

At Hilton *A. scutellaris* has year after year been found nesting in aggregations in the floor of a sandpit (Fig. 2). Within the sandpit it selects sites where the complete removal of the overlying sandy alluvial soil has exposed the underlying subsoil which, although itself of a sandy nature, is very fine and compact and contains a considerable clay factor making it malleable when mixed with water. The selected sites in addition are bare and weathered, not freshly exposed.

Two further nests were found at Hilton on the earthen bank of a furrow at some little distance from the sandpit in an area of clayey soil.

Flight period

The flight period in the Grahamstown area, as ascertained from Malaise trap catches made at Hilton (1970–71 and 1975–76), at Table Farm (1970–71) and at Belmont Valley and Howison's Poort (both 1971–72), is from the beginning of November until the end of March. Nesting is well advanced by the second week in November and continues throughout the flight period.

Flowers and young plant growth visited

A. scutellaris was captured on the flowers of *Lasiospermum bipinnatum* (Thunb.) Druce (Asteraceae) growing on the bank of a furrow which passes above the sandpit (3.xi.1977, 1 male; 10.xi.1977, 2 females and 1 male; 15.xi.1977, 1 female, all F.W.Gess) and on the flowers of *Selago corymbosa* L. (Selaginaceae) growing in the sandpit (1 female, 2.xii.1977, R.W.Gess).

Identification of prey and location of sting sites

A. scutellaris at Hilton was found to prey exclusively upon larval Pyralididae. Forty-one prey were recovered from nests. Two species were taken: one, with longitudinal reddish stripes and five pairs of prolegs, was represented by thirty-eight specimens; the other, without definite markings and with only two pairs of prolegs (on the sixth and on the last abdominal segements), was represented by three specimens. Neither species could be identified beyond the family. Other than for three prey of the more common species, which were partly devoured and were represented by shrunken remains, all the caterpillars were alive and responded to tactile stimulation. In length the thirty-eight measurable prey varied between 3,0 and 10,0 mm (average 6,3 mm; 76% between 4,1 and 7,0 mm).

Fig. 2. Sandpit, Hilton, 16.xi.1975; figures at site of nesting aggregation of *Antepipona scutellaris* Giordani Soika.

Eighty sting sites, indicated by dark lesions, were located ventrally on thirty-seven prey and were found to be distributed as follows: thirty-three in the region of the neck, two on the mesothorax posterior to the legs, five on the metathorax anterior to the legs, one on the metathorax between the legs, thirty-three on the metathorax posterior to the legs, two on the first abdominal segment and four on the second abdominal segment. The favoured target areas for stinging are clearly the neck and the metathorax posterior to the legs. Stings in other but nearby areas probably represent cases in which the target areas have been missed.

Description of nest

The nest of *A. scutellaris* consists of a subterranean burrow surmounted by a mud turret which is a vertical flared or funnel-shaped tube (Figs 3 and 4). The burrow consists of a shaft of the same diameter as the base of the turret terminating in a single cell or branching to terminate in two cells (Fig. 4 a-d). No nest was found with more than two cells. However, as none of the nests was sealed it is possible that further cells might have been constructed had the wasps' activities not been terminated by the destruction of their nests.

Method of construction of nest, oviposition and provisioning

Water, which is required for nest excavation, is fetched in the crop.

A nest site having been chosen, nest construction is initiated by the moistening of the ground with water to form mud which is then excavated in the form of pellets. Pellets are laid down around the shaft initial in such a way that the base of the turret will have the same inner

diameter as that of the shaft, that is 4–4,5 mm (average 4,1, sample of 14). Additional pellets are laid down in such a way that the diameter of the turret increases resulting in its being flared. Final turret height is 5–8 mm (average 6,2 mm, sample of 13) and the distal diameter is 5–7,5 mm (average 6,3 mm, sample of 13). The outer surface of the turret is left rough but the inner surface is smoothed.

After the completion of turret construction, mud pellets extracted in excavation are discarded in a distinct pellet dropping area 60–90 cm from the nest. When leaving the nest with a pellet, the female flies an elliptical path and always returns to the nest on the same side. She will be diverted from her regular path by an intruder as she will try to chase it off. For example a female wasp was observed making successive short downwards flights at a tiger beetle, *Cicindela brevicollis* Wied. (Cicindelidae), which was 25 cm from her nest.

The main shaft which is constant in diameter descends vertically and terminates at a depth of 53–89 mm (average 70 mm, sample of 14) in a cell 10–20 mm long, somewhat ovoid, having a diameter greater than that of the shaft (Fig. 4a).

A cell having been excavated, the wasp enters the nest backwards and oviposition takes place. An egg, pale straw yellow, slightly curved, 2,9–3,3 mm (sample of 5) and 0,8–0,9 mm at mid-length, is suspended from the ceiling of the cell on a short filament, 0,8 mm long.

After oviposition into the empty cell provisioning begins. In the sample up to thirteen prey were found to have been provided per cell. Provisioning having been completed the cell is sealed with a mud plate which may be followed by earth and a second mud plate cutting it off from the shaft at the point where curvature began (Fig. 4c). The shaft is then continued and terminates in a second similar cell at a depth somewhat greater than that of the first (Figs 4c and d). After this cell has been supplied with an egg and provision it is sealed and again the seal may be followed with earth and a second seal (Fig. 4d).

Seventeen nests were investigated, of these three nests had no cells, twelve nests each had

Fig. 3. Female *Antepipona scutellaris* Giordani Soika, standing on the mud turret surmounting her burrow, Hilton, 11.xii.1975. (× *c* 2,6)

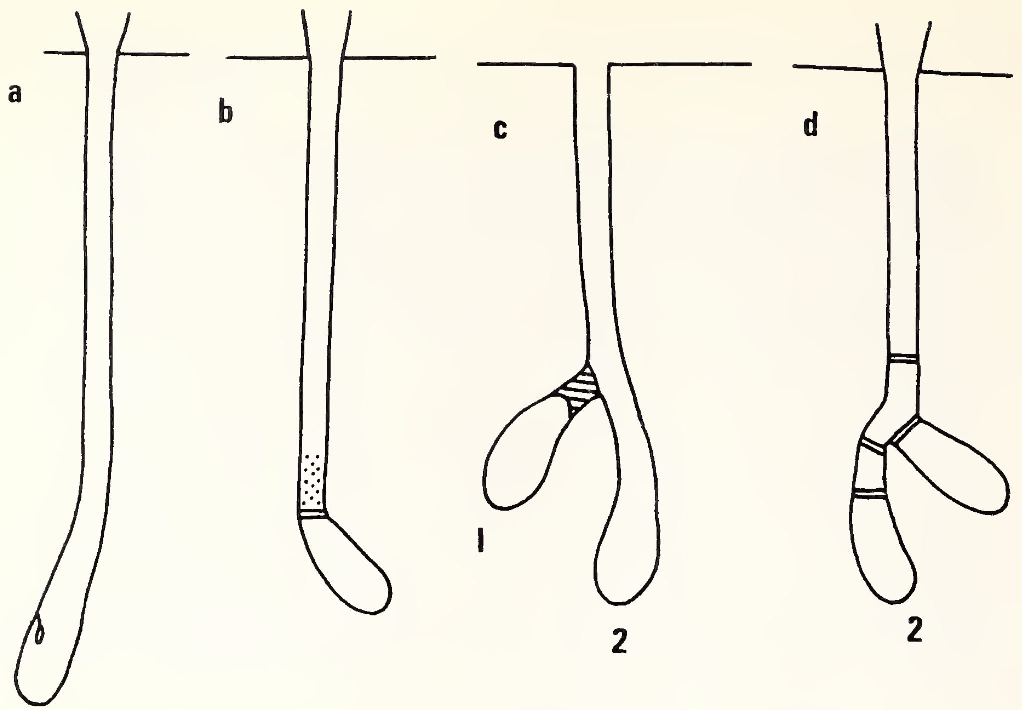

Fig. 4. Vertical plans of four nests of *Antepipona scutellaris* Giordani Soika, Hilton, 12–23.ix.1975. (× 1) Numbers indicate sequence of construction of cells.

a single cell and two nests each had two cells. As none of the 17 nests excavated had been finally sealed it is not known whether more than two cells may be excavated.

Sleeping and sheltering behaviour of adult wasps

Adult female wasps shelter in their nests after work ceases in the afternoon and during the day, when weather conditions are unsuited to normal nesting activities. A nest opened up after a period of rain was found to contain a sheltering female below a plug of water-borne earth. A sheltering or sleeping female positions itself in the nest shaft, facing the entrance. In order to achieve this position the female enters the nest backwards, as when entering to oviposit. As a temporary closure is not made at the end of the working day, the presence of the wasp in the nest serves as a protection to an egg or young larva and provision within an open cell, particularly as it is common for there to be an open cell at the end of the working day.

Associated insects

Nest parasites were found in the second cell of both of the two-celled nests of *A. scutellaris* investigated. All other cells were free of parasites.

One of the affected cells contained a second instar (caraboid) larva of the family Meloidae (Coleoptera). Rearing the larva was attempted but unfortunately failed. The presence of the

meloid is of interest as nests of another eumenid, *Parachilus insignis* (Saussure), investigated at Hilton (Gess and Gess, 1976) were found to be parasitized by a meloid, *Lytta enona* Péringuey, which in its larval stage fed upon the caterpillars laid in as provision by its host for its own young.

The other affected cell contained two small foreign larvae the identity of which could not be determined. In both cells the *Antepipona* larva was still alive. Rearing the larvae was attempted but unfortunately failed.

Three instances of usurpation of *A. scutellaris* nests by a megachilid bee, *Megachile (Eutricharaea) meadewaldoi* Brauns were recorded. These bees constructed cells from petals of a violet flowered *Wahlenbergia* species (Campanulaceae) growing in the sandpit. This bee has also been recorded from Hilton nesting in old or abandoned burrows of *Bembecinus oxydorcus* (Handlirsch) (Gess and Gess, 1975) and *Parachilus insignis* (Saussure) (Gess and Gess, 1976).

Euodynerus euryspilus (Cameron)

Geographic distribution

Euodynerus euryspilus (Cameron) is widespread in southern Africa.

Description of nesting sites

No natural nests of *E. euryspilus* have been located. However, four nests in trap-nests were obtained from Hilton. All the trap-nests utilized were situated at heights of 25–100 cm above the ground and were attached to branches of the woody shrub or small tree *Acacia karroo* Hayne (Leguminosae: Mimosoideae) growing in the clay areas above and below the furrow and on the flats below the furrow. Natural nesting sites will therefore almost certainly prove to be pre-existing cavities such as abandoned beetle borings in the branches of bushes of thorn scrub and small trees along the river banks.

Flight period

E. euryspilus flies at Hilton from October to March.

Flower visiting

There are no records of flower visiting for this species from Hilton. Both females and males have, however, been recorded visiting the flowers of *Acacia karroo* Hayne (Leguminosae: Mimosoideae) at two other localities: 2 females, 1 male, Colesberg, 16–17.i.1985, D. W. Gess; and 1 male, Oudtshoorn, 9–12.xii.1986, F. W. Gess.

Identification of prey and location of sting sites

The cells of the nests examined were provisioned with caterpillars belonging to the family Pyralididae (Lepidoptera). In two nests provisioned during November 1973 the caterpillars were identified as those of *Loxostege frustalis* Zeller, the Karoo Caterpillar, a serious pest of *Pentzia incana* (Thunb.) Kuntze (Asteraceae). Prey caterpillars ranged in length from 12–16 mm and numbered from 7–13 per cell, depending upon their size. They were partially paralysed and were very tightly packed into the cells. Fourteen caterpillars were examined for sting sites. All bore at least one sting clot on the prothorax anterior to the legs—that is in the neck region, two bore sting clots on the mesothorax posterior to the legs, ten bore sting clots on the metathorax (generally posterior to the legs) and five bore sting clots on the first abdominal segment. All the sting clots were on the ventral surface.

Description of nest

The four nests of *E. euryspilus* in trap-nests consisted of linearly arranged cells, in three instances preceded by a preliminary plug and in the only completed nest succeeded by a vestibular cell and a final seal. The preliminary plugs, cell closures and the final closure were all of mud; the cell walls were unlined.

Method of construction of nest, oviposition and provisioning

A large number of trap-nests with borings of 4,8 mm, 6,4 mm, 9,5 mm and 12,7 mm were offered in mixed bundles in a wide variety of situations at Hilton. Four were accepted for nesting by *E. euryspilus*; three were 6,4 mm borings and the fourth was a 9,5 mm boring.

The building material introduced into the nest was in all cases a reddish clayey mud.

In three of the four trap-nests a preliminary plug had been constructed at or near the blind end of the boring. In two of these nests this plug consisted of a thin layer of mud filling in the corners and rounding off the end to form a smooth concave surface; in the third an empty space 10 mm long was left between the end of the boring and the 3 mm thick preliminary plug which was separated from the first provisioned cell by a 13 mm long empty cell.

The cell walls were not lined.

A cell having been prepared for oviposition, a pale yellowish-white egg is suspended by a thin filament from the roof of the cell at the inner end of the latter. Egg length ranged from 2,7–3,3 mm (average 3 mm, sample of 4) and egg width from 0,84–0,92 mm (average 0,88 mm, sample of 4). The filament was 0,56–0,60 mm long.

Provisioning takes place after oviposition. The prey caterpillars are tightly packed into the cell. Completed cells contained 7–13 caterpillars, depending upon size.

After provisioning has been completed the cell is sealed with a mud plate, 1–2 mm thick. In no nest were intercalary cells present. In all nests the inner end of a succeeding cell was the seal of the previous cell.

Only one of the nests had been completed. It contained two sealed provisioned cells and a 118 mm long vestibular cell between the outer provisioned cell and the 3 mm thick closing plug which had been constructed just within the trap-nest opening. The two provisioned cells filled only 22,5% of the total length of the boring. The other three nests were incomplete and contained respectively one sealed provisioned cell and one still open and partially provisioned cell; two sealed provisioned cells; and four sealed provisioned cells.

The measurements of the sealed cells irrespective of the sex of the wasp for which they were constructed are summarised in Table 1.

TABLE 1.

Measurements of sealed cells of *Euodynerus euryspilus* (Cameron) in trap-nests of different sizes irrespective of the sex of the wasp for which they were constructed.

Boring diameter (mm)	No. of cells	Range in length (mm)	mean length (mm)
6,4	5	15–29	23,0
9,5	4	10,5–15	13,6

Life history

Cell construction and cell provisioning in the four trap-nests utilized by *E. euryspilus* took place during the second half of November, 1973 (2 nests), during the second half of February, 1975 (1 nest) and during the second half of February, 1977 (1 nest).

Due to parasitism and other causes no *E. euryspilus* were reared from the nine cells and developmental details for the species are thus meagre.

In all cases the egg hatched about three days after oviposition and the larva began feeding on the prey lying immediately below it at the inner end of the cell.

Sheltering behaviour

During inclement weather females were found sheltering in their nests, facing outwards. Doubtless they also spend the night in their nests.

Associated insects

Chrysis hoplites Mocsáry (as *Octochrysis hoplites* in Gess, 1981) (Chrysididae) was reared from six of the nine cells of *E. euryspilus*.

Some observations were made on three of the cells parasitized by *C. hoplites*. All the cells were provisioned during the second half of November 1973. In each cell the larva of *E. euryspilus* hatched successfully and commenced feeding upon the stored provision. Within a day or two of hatching the chrysidid larvae of about the same size as those of *E. euryspilus* were seen in the cells, one each in two of the cells and two in the third cell. By the third day after their hatching the host larvae had been killed and eaten. In the cell in which there were two *C. hoplites* larvae, the killing and eating of the host larva was followed a day later by one of the chrysidid larvae eating the other. When only one chrysidid larva remained in each cell the stored provision was eaten.

Cocoon spinning by the three *C. hoplites* larvae, which took about two days, was completed 15–17 days after the provisioning of the host's cell and thus 12–14 days after the hatching of the host's larva from the egg. Two of these *C. hoplites* emerged as adults during the same summer, 41 and 42 days after the date of cocoon spinning, the third underwent diapause and emerged as an adult the following summer, 364 days after cocoon spinning.

Toxophora australis Hesse (Bombyliidae) was reared from a single cell provisioned during the second half of November, 1973. There was no indication of its presence until 53 days after cocoon spinning by its host was completed when its motile pupa, aided by its strong cephalic spines broke through the mud cell wall and progressed along the length of the nest to its opening. Within two minutes of the pupa's escaping from the trap-nest into the open the pupal skin was seen to split down the back and the adult fly, a male, emerged. The wings expanded within a few minutes. It is not clear whether the host was *E. euryspilus* or *C. hoplites* but it seems more likely to have been the latter.

Chrysis species and *Toxophora* species are recorded by Krombein (1967) as parasites in the nests of *Euodynerus* species in North America.

Rhynchium marginellum sabulosum **(Saussure)**

Geographic distribution

Rhynchium marginellum sabulosum (Saussure) is widespread and common in the Afrotropical Region.

Description of nesting sites

R. m. sabulosum nests in pre-existing cavities above ground level in close proximity to a supply of water and clayey soil.

At Hilton four nests were obtained, each constructed in a 9,5 mm bore trap-nest. These trap-nests were constituents of a bundle tied together and positioned horizontally in a space in a north facing river bank. This bank is of recently mineralized fine sand in which there are numerous pre-existing galleries (Gess 1981, Fig. 27) which are most probably natural nesting sites of this wasp.

In order to base the description of the nest on a larger sample a further thirty nests of *R. m. sabulosum* obtained from a garden in Grahamstown are included. Eighteen were in trap-nests of bore 6,4 mm, 9,5 mm and 12,7 mm placed horizontally 174 cm above the ground. Eleven were in cut reeds, the culms of *Arundo donax* L. (Gramineae), of bore 12–19 mm. Of these seven were 5–30 cm above ground and were constituents of a horizontally placed bundle and four were part of a bean frame and varied in angle from 0–70° with the horizontal and in height from 117–190 cm above the ground. As the reeds had been cut at different distances along the internodes the available nesting cavities varied in length. Successful nests were made in cavities from 7–25 cm in length. The thirtieth nest was in a fence post, in a 12,7 mm boring 76 cm above the ground.

Flight period

R. m. sabulosum, in Grahamstown, is actively nesting by the first week in December and continues into April.

Flower visiting

The authors are aware of only one record of *R. m. sabulosum* visiting flowers: one male on flowers of *Sarcostemma viminale* (L.) R. Br. (Asclepiadaceae), Kommadagga, 14.i.1986, R. W. Gess.

Identification of prey and location of sting sites

Over four hundred prey caterpillars were examined and all belonged to the Pyralididae. Thirteen of these prey caterpillars were from Hilton and were unstriped and bright green. The remainder were from the Grahamstown sample and were of two forms—one longitudinally striped and brown and one unstriped, bright green and identical with those from Hilton. These probably represent two species.

The number of caterpillars constituting the provision for a single cell varied according to the size of the individual caterpillars. At the beginning of the season the provision consisted of four or five large brown caterpillars, 14–25 mm long. As the season advanced there was a drop in the size of this caterpillar prey and the number per cell rose to up to thirteen. From 13.i.1975–2.ii.1975 both the brown and the green caterpillars were present in any one cell after which only the green caterpillars, smaller than the smaller brown caterpillars, were present and sixteen to thirty-one were supplied per cell.

Sting sites were located in a total of thirty prey. All bore at least one sting on the prothorax in front of the legs (that is in the neck region), most bore stings on the metathorax behind the legs and/or on the first abdominal segment, and a few in addition bore stings on the mesothorax behind the legs. All sting sites were situated on the ventral surface.

All prey found in the cells were alive, continued to defaecate and responded to tactile stimulation.

Description of the nest

The nest of *R. m. sabulosum* is constructed in a pre-existing cavity and consists of a number of serially arranged cells each sealed with a mud plug, frequently separated by intercalary cells and succeeded by a vestibular cell which may be subdivided and is closed by a thick usually layered mud plug which seals the nest entrance (Fig. 5). When the inner end of the boring is uneven or when the boring is not circular in cross section mud is used to make modifications (Fig. 5c and d). In order that the cells should be of adequate volume their lengths vary according to the diameter of the boring used. Furthermore cells which will cradle female wasps are larger than those which will cradle male wasps (Table 2). The diameter of the boring in the lower ranges becomes a limiting factor, only males being produced in 6,4 mm borings.

TABLE 2.

Measurements of sealed cells of *Rhynchium marginellum sabulosum* (Saussure) in trap-nests of different sizes, showing the relationships between cell length, boring diameter and the sex of the wasp for which the cell was constructed.

	Cells from which male wasps were reared			Cells from which female wasps were reared		
Boring diam. (mm)	No. of cells	Range in length (mm)	Mean length (mm)	No. of cells	Range in length (mm)	Mean length (mm)
6,4	6	25–42	34,7	0	–	–
9,5	10	16–27	21,4	7	22–32	27,1
12,5	13	15–25	19,7	12	20–33	25,8

Method of construction of nest, oviposition and provisioning

Nest construction is initiated by the wasp's selecting a suitable pre-existing cavity and cleaning out any small pieces of debris and spider spinnings. If, as in *A. donax* culms, the inner end of the cavity is firm, smooth and concave no further preparation is required before oviposition (Fig. 5a and b). However, if the inner end of the cavity is uneven, angular or rough, the wasp first constructs a preliminary plug with mud applied directly to it (Fig. 5c) (16/22 in the sample of trap-nests). Furthermore, if some foreign object such as extensive spider spinnings obstructs the inner end of the boring, a preliminary plug is constructed to seal it off (Fig. 5d) (6/22 in the sample of trap-nests).

Mud for the construction of the preliminary plug and subsequent plugs is obtained by the wasp from a dry quarry site, the water for mixing the mud being carried there in her crop from a selected water source. The horizontal distance from the nests to the quarry sites in the three

cases where these were located were 12 m, 7,5 m and 7,7 m respectively. In two of these cases the water sources were also identified and were 7 m and 3,7 m from the quarry sites and 4 m from the nests. The nest, the quarry, and the water source in each case formed the corners of a triangle. The wasp having filled her crop with water flies with it to the quarry where she regurgitates it and kneads it into the earth to form mud which she gathers together with her mandibles to form a pellet against her front legs which support it from behind and below. Supporting the pellet in this way and holding it with her mandibles she flies with it to the nest. On alighting at the nest the pellet is held by the mandibles only. Two large pellets are made for each crop-full of water and each is approximately 6 mm in diameter. The route taken between the nest and the quarry is eliptical, the wasp following one long side of the curve on the outward journey and returning along the other.

The preliminary plug, when present, having been completed the wasp oviposits. The egg is yellow, gently curved, in average 3,6 mm in length and 1,1 mm in diameter at mid length (sample of 6) and is suspended from the roof or side of the cell so that it hangs down on a short filament. The egg is always positioned towards the inner end of the cell.

Oviposition having taken place hunting commences. The wasp captures a prey caterpillar and subdues it by stinging it several times. She then transports it to her nest in flight clasped beneath her body with her legs and held by her mandibles near its head end. The caterpillar is orientated with its head facing the direction of travel and with its venter uppermost. Retaining the prey in this position the wasp drags it into the nest. Successive prey are added to the cell until it is fully provisioned. Within the cell the prey are not arranged in any set pattern, that is some face the inner end of the cell and some the outer end. Provisioning of a cell having been completed it is sealed with a mud plug 2,5–5,5 mm thick at its edges and 1–2 mm thick towards its centre. Before proceeding with oviposition into and provisioning of another cell the wasp may construct an empty intercalary cell.

One to three intercalary cells were present in each of 15 nests of the 25 nests having two or more provisioned cells. The intercalary cells had been constructed singly between pairs of provisioned cells in all but one instance in which a pair was present (Fig. 5c). The intercalary cells ranged in length from 3–20,6 mm.

After the full number of cells has been completed the nest is sealed by the construction of a thick, layered mud plug which is usually positioned at the entrance to the cavity leaving a vestibular cell which may be subdivided by partitions (Fig. 5). In the sample of 25 nests the length of the vestibular cells ranged from 5–130 mm and the plug from 5–32 mm.

Female sleeping and sheltering habits during nesting

It was found that the female of *R. m. sabulosum* regularly spends each night within her nest, her head facing the open end, a position which she also takes up when weather conditions are unsuited for normal nesting activities.

As the wasp at no time constructs a temporary closure to the nest and as the end of her working day is determined by the temperature or light intensity or both and not by the completion of any particular phase of nesting (such as the sealing of a cell), the retirement of the wasp to the nest during the night and during unfavourable weather conditions not only serves to give it shelter but equally importantly ensures the safety of the egg and of any prey caterpillars which may be present in an unsealed cell. It was in fact common to find a wasp sleeping or sheltering in a nest with an open cell containing an egg or an egg and a number of prey. In one instance a wasp spent the night in very cramped quarters, straddling the prey caterpillars, in a

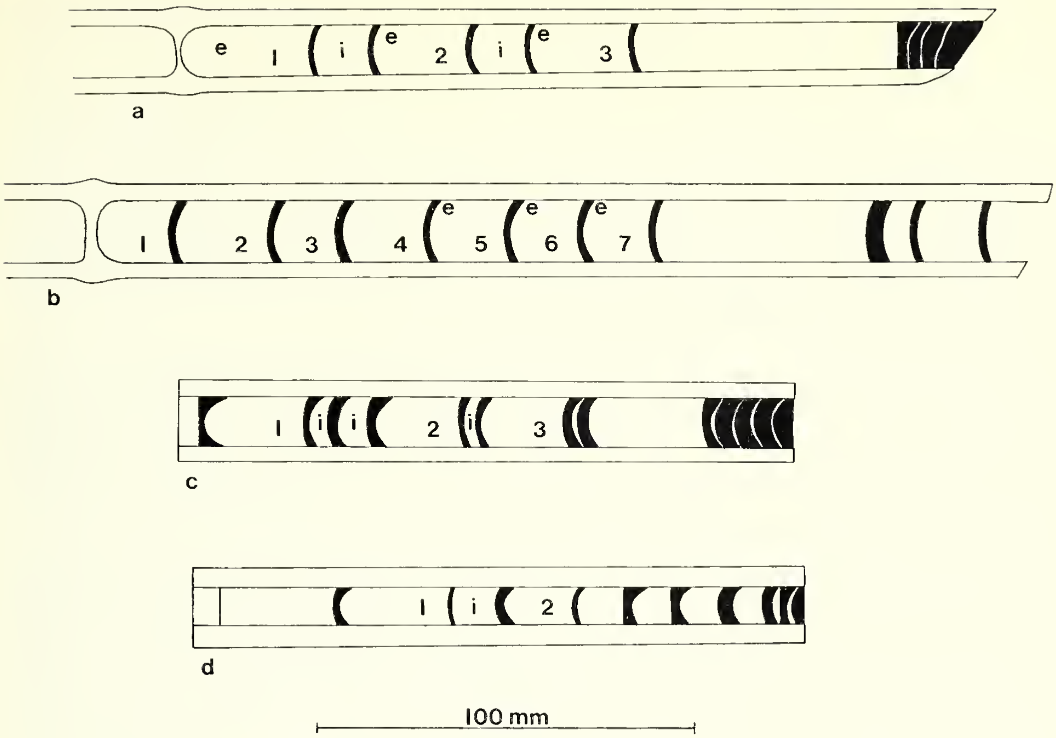

Fig. 5. Vertical plans of four nests of *Rhynchium marginellum sabulosum* (Saussure): (a and b) nests in cut culms of *Arundo donax* L. (Gramineae), Grahamstown i/ii.1975; and (c and d) nests in trap-nests, "sandstone" bank, Hilton, 21.ii.1975. Numbers indicate sequence of construction of cells; e indicates presence of and position of egg; and i indicates interstitial cell.

fully provisioned but unsealed cell situated so close to the nest opening that the wasp was barely under cover. Cell closure and nest sealing were completed early the following morning. It thus seems that this behaviour could as much be guarding behaviour as sheltering behaviour.

Life history

In the present study it was found that the time taken from oviposition to the hatching of the egg took two to three days.

For a sample of 19 larvae developing under laboratory conditions the time taken from the hatching of the egg to the attainment of larval maturity was five to six days, occasionally seven days, and from larval maturity to the commencement of spinning one or two days, occasionally three.

Pupation took place after a further eight to sixteen days and emergence 18 to 25 days later. Males in individual nests emerged 1–5 days before females ensuring that the males in the outer cells emerge before the females in the inner cells.

When a mature larva commences spinning it lines the cell with a layer of yellow cellophane-like material composed of "varnished" spinnings with a characteristic aromatic scent.

The nests from Hilton yielded four females and two males which emerged from the third week in March to the first week in April. Those from Grahamstown yielded thirty-one females and thirty-five males which emerged from the first week in February to the first week in April.

It seems likely that adults emerging before the end of the nesting season must nest and produce a second generation of wasps which would overwinter in the pre-pupal stage as it is highly unlikely that *R. m. sabulosum* would overwinter in the adult stage and furthermore no adults have been recorded in the Grahamstown area after April and before December. It seems highly likely therefore that *R. m. sabulosum* is bivoltine.

Sequence of sexes in nests

Certain species of aculeates which construct serially arranged cells within pre-existing cavities commonly show a fixed sequence of sexes in nests in which both males and females develop. This has been shown by Krombein (1967: 29) for species of Vespidae and some Megachilidae and by Gess and Gess (1982: 165–166) for a species of Sphecidae, *Isodontia pelopoeiformis* (Dahlbom). To establish whether this is also true of *R. m. sabulosum* an analysis was made of 19 completed nests of at least two cells, 14 in 12,7 mm bore trap-nests and 5 in reeds.

Of the 19 nests analysed 2 two-celled nests and 1 three-celled nest produced all males and three yielded no information concerning the correlation between the position of the cell within the nest and the sex of the wasp produced within that cell. In the remaining 15 nests, 5 two-celled, 5 three-celled, 4 four-celled and 1 eight-celled, females had without exception developed within cells constructed and provisioned before those in which the males developed. Female producing cells are therefore sited towards the inner or blind end of the nesting gallery and male producing cells towards the outer or open end of the gallery. It follows that, if the first cell in a nest is male producing, all subsequent cells constructed within that nest will also be male producing.

Associated insects

No parasites of *R. m. sabulosum* were recorded. However, some cells in which the wasp's young failed to develop yielded instead foreign insects. Thus a single individual of a small species of Braconidae was reared from each of two cells of one nest and a single individual of a small species of Tachinidae was reared from one cell of another nest, both nests being from Grahamstown. It seems probable that the presence of these foreign insects in the cells resulted from the inclusion amongst the caterpillars introduced into the cells as provision of individuals which had already been parasitized by Braconidae and Tachinidae.

Tricarinodynerus guerinii (Saussure)

Geographic distribution

Tricarinodynerus guerinii (Saussure) is widespread in its distribution in tropical and southern Africa and appears to be able to exist in a wide range of climatic conditions. It is represented in the collection of the Albany Museum by specimens from all four provinces of South Africa as well as from Lesotho. The species shows considerable variation in its coloration

and this has lead some authors to split it into a number of so-called subspecies which do not, however, appear to have any real validity. The wasps concerned in the present study are of the colour pattern associated with the "subspecies" *rubens*.

Description of the nesting sites

T. guerinii nests in suitable pre-existing cavities above ground level in close proximity to a supply of water and clayey soil. At Hilton three nesting sites were located along the course of the New Year's River at heights reached by water only during times of flood. Each of the nesting sites is different with respect to the geological nature of the material in which the nests occur and with respect to aspect.

The most frequented site consists of a west facing bank of firmly compacted very fine sand. Erosion of the bank has exposed the roots of various shrubs and trees growing above the water course and has cut through a number of subterranean cavities of uncertain origin (Fig. 6).

The second most frequented site is a bank of north facing crumbly sandstone-like material probably formed by recent mineralization of a fine sand similar to that at the first site and referred to as the "sandstone" bank (Gess, 1981, Fig. 8).

The least favoured site is a south east facing cliff cut across the roughly horizontal bedding of a shale formation (Fig. 7).

In the sand bank and the "sandstone" bank the pre-existing cavities utilized are burrows made in previous years by nest excavating Hymenoptera (Fig. 9). A preference is shown for holes in sheltered positions such as the upper parts and sides of cavities in the sandbank (Fig. 8) and in a gap between the "sandstone" bank and a "sandstone pillar" separated from the bank by weathering. On the shale cliff nesting is in crevices occurring within and between layers of shale.

Nesting sites of *T. guerinii* have also been located by the authors at Tierberg, Prince Albert where they were situated in sheltered positions in a recently mineralized eroded river bank and in mud walls inside a ruined mud walled building close to the river. In both instances the gallery initiators were solitary bees.

Empty cells of aerial mud nests of *Sceliphron* (Sphecidae) and *Synagris* (Eumenidae) are used for nesting at False Bay, Lake St Lucia, Natal (Weaving, 1990, pers. comm.).

At Hilton bundles of trap-nests were lodged in cavities in the sandbank, in the gap in the "sandstone" bank and in cracks in close proximity to natural nests in the shale cliff. Only one trap-nest of 12,7 mm bore was accepted. It was sited in the shale cliff.

This low incidence of acceptance of trap-nests is not attributable to the very different nature of the substrate as Weaving (pers. comm., 1990) found *T. guerinii* nesting extremely abundantly in cut reeds used in buildings at False Bay.

Flight period

T. guerinii flies at Hilton from early November, in which month a pair in copula was observed resting on the face of the "sandstone" bank. Nesting was observed in January and February but undoubtedly starts earlier in the summer.

Nesting at Tierberg was in progress in late November/early December.

T. guerinii appears to be univoltine at Hilton.

Flower visiting

At Hilton both sexes of *T. guerinii* have been collected on flowers: Celastraceae: *Maytenus*

Fig. 6. Sand bank, eroded bank of very fine compacted sand, NewYear's River, Hilton, 15.ii.1974.

Fig. 7. Cliff cut across roughly horizontal bedding of shale formation by New Year's River, Hilton, 1974.

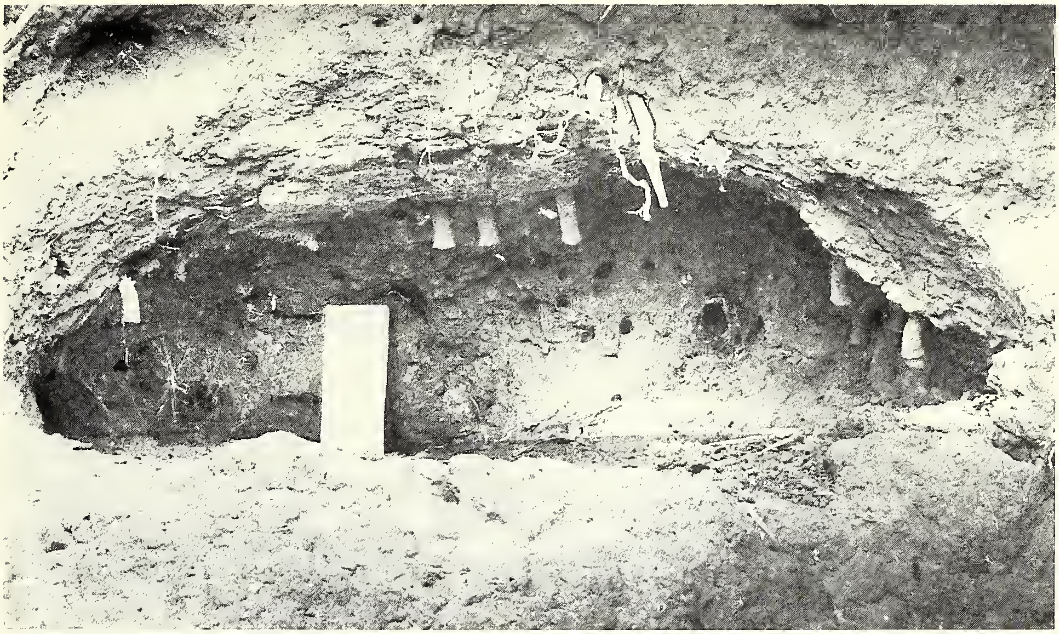

Fig. 8. Close view of cavity in sand bank showing eight *Tricarinodynerus guerinii* (Saussure) turrets, Hilton, 15.ii.1974. (× 0,25)

Fig. 9. Mud turret and nesting gallery (cut through vertically) of *Tricarinodynerus guerinii* (Saussure), "sandstone" bank, Hilton, 27.i.1975. (× 1,3)

linearis (L. *f.*) Marais, 1 female and 1 male, 11.xii.1969, F.W.Gess; and Leguminosae: Mimosoideae: *Acacia karroo* Hayne, 1 male, 15.ii.1974, F.W.Gess. Both plants were growing near the sandbank nesting site.

Other flower visiting records from specimens in the Albany Museum collection are:

Leguminosae: Mimosoideae: *Acacia caffra* (Thunb.) Willd., 2 males, Oudtshoorn, 9–12.xii.1986, F.W. Gess; 1 male, Oudtshoorn, 9–12.xii.1986, R.W. Gess. *Acacia karroo* Hayne, 1 male, Colesberg, 17.i.1985, D.W. Gess.

Leguminosae: Papilionoideae: *Calpurnia glabrata* Brummitt, 1 male, Mamathes, Lesotho, 2.xi.1952, C.F. Jacot Guillarmod.

Umbelliferae: *Foeniculum vulgare* A.W. Hill, 1 male, Alexandria/Salem, H.W. Gess.

Rhamnaceae: *Ziziphus mucronata* Willd., 2 females, 1 male, Adelaide, C.F. Jacot Guillarmod.

Identification of prey and location of sting sites

From Hilton seven specimens of prey were obtained from three open cells of nests in the "sandstone" bank, all were small reddish caterpillars, probably Tortricidae, and ranged in length from 8—11 mm. All the caterpillars were alive and responded to tactile stimulation. Sting sites were recorded for six of the prey. All were on the ventral surface. All prey had been stung in the region of the neck and on the metathorax posterior to the legs. In addition one had been stung on the mesothorax anterior to the legs and another on the mesothorax posterior to the legs.

Description of nest

The nest of *T. guerinii* is characterized by a downwardly curved ribbed mud entrance turret most commonly slightly flared at the distal opening (Figs 8–13).

Within (Fig. 13) are several cells arranged, depending upon the shape of the pre-existing cavity which forms the nesting gallery, either in a linear series (Fig. 13g) or radiating from the inner end of an entrance burrow (Fig. 13f).

The degree of modification of the cavity is determined by its suitability for cell construction. The cavities in the sand and in the "sandstone" are old burrows and are therefore circular in cross section. In these very little mud is used for smoothing the walls whereas in the irregular shaped crevices in the shale a greater amount of mud is required to round off unevennesses and to create cells and an entrance passage.

The size of the nest is not necessarily determined by the available space as a preliminary plug may be constructed reducing the depth of a deep cavity (Fig. 13h). Each cell is sealed by a thin mud plug and the last cell is separated from the closing plug by a vestibular cell (Fig. 13c, e and g). In addition to the plug closing the gallery the entrance turret is sealed at its distal opening (Figs 12 and 13c-g) and may be divided along its length by additional mud partition (Fig. 13g).

Method of construction of nest, oviposition and provisioning

Nest construction is initiated by the selection of a suitable cavity for use as a nesting gallery. The wasp flies off and returns with a load of mud which she lays down either around the rim of the entrance to the gallery or a short distance inside the entrance to the gallery. With successive loads of mud she first constructs a foundation ring. If the entrance to the cavity is of suitable diameter, this will be reflected in the diameter of the turret. If, however, the diameter is too

Fig. 10. Three mud turrets of *Tricarinodynerus guerinii* (Saussure) to show curvature and surface texture. (× 1,28)
Fig. 11. Adult *Tricarinodynerus guerinii* (Saussure) (male above, female below) and mud turret showing outer closure. (× 1, 35)
Fig. 12. Trap-nest furnished with a mud turret of *Tricarinodynerus guerinii* (Saussure), Hilton, 11.i.1975. (× 0,95)

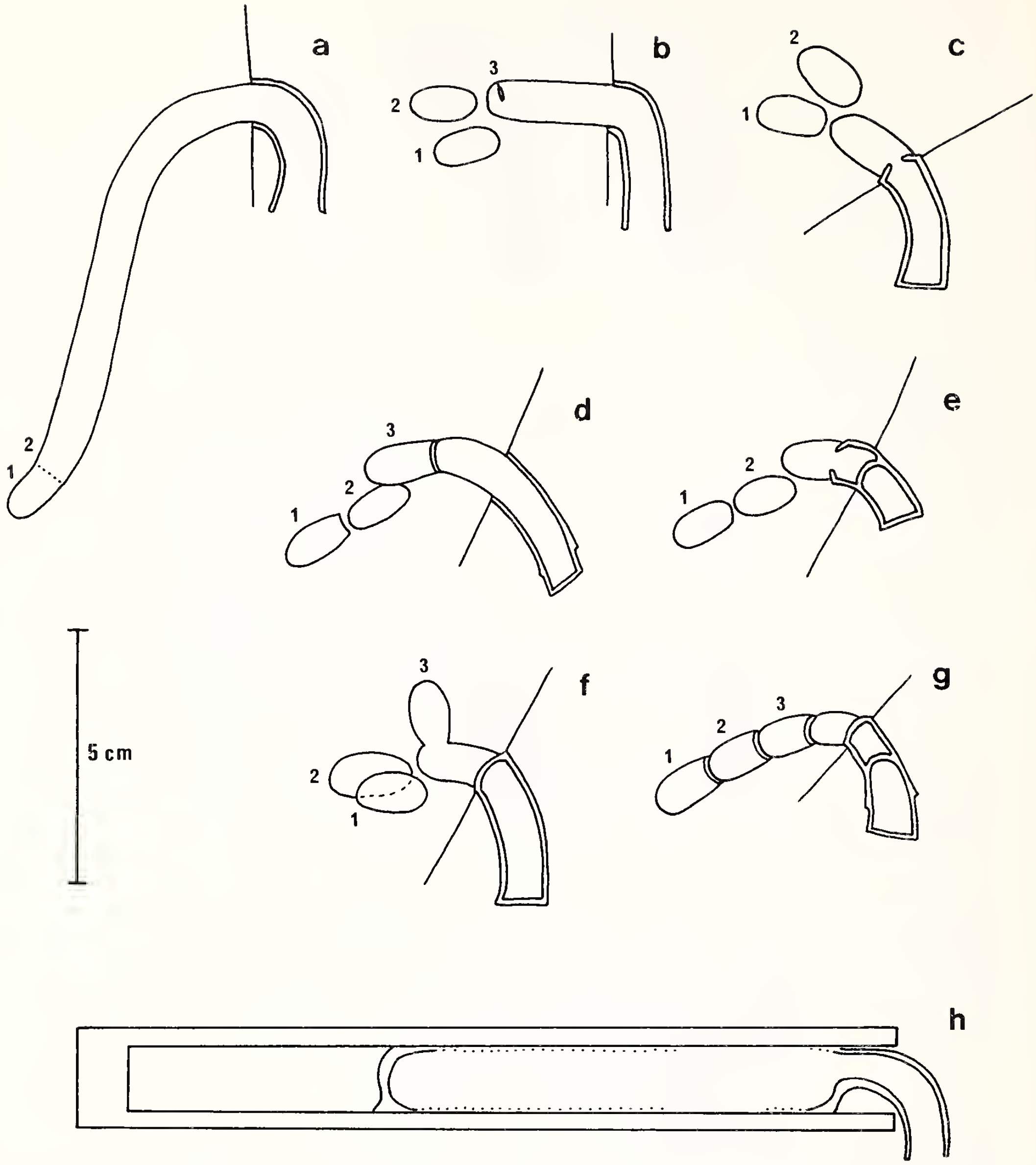

Fig. 13. Vertical plans of eight nests of *Tricarinodynerus guerinii* (Saussure): (a–g) showing sequence of cell construction and provisioning of seven nests in sand bank, New Year's River, Hilton, 15.ii.1974 and (h) showing preliminary gallery modifications of a 12,7 mm bore trap-nest, Hilton, i.1974.

large as was the case in the 12,7 mm bore trap-nest used for nesting, the opening will be partly closed to reduce it to a suitable diameter, 5,5–8 mm, before turret construction proceeds (Fig. 13h). As turret construction advances the wasp carefully smoothes the inner surface of the walls but leaves the external surface rough-cast giving the turret its characteristic ribbed and knobbly appearance Figs 11–12). No interstices are left. Either immediately after the first ring of the turret has been laid down or after a short horizontal section of tube has been constructed, the structure is added to unevenly; the layering away from the bank being wider than that towards the bank so that the tube curves over and downwards. If the tube reaches the vertical plane, curvature ceases but further additions may be made to extend its length which in the sample was up to 31 mm. The final section of the tube may be laid down in such a way that the rings are of increasing diameter causing the tube to be flared towards its distal opening.

The wasp prepares the first cell using mud to make the neccessary modifications to the gallery. The first cell having been prepared a yellow, very slightly curved egg is laid suspended from the ceiling on a short filament (Fig. 13b). Two of the four eggs found were measured, one was 2,8 mm long and 0,9 mm wide at mid-length and the other was 3,1 mm long. Each was suspended on a filament 0,2 mm long.

Hunting then commences. The wasp captures a prey caterpillar, stings it and flies to her nest with it held by her mandibles, supported beneath by her legs and facing the direction of travel. On reaching the nest she enters rapidly.

As the cells examined were either still open and only partially provisioned or were sealed but contained fully grown larvae and no prey, no information is available on the number of or weight of prey with which each cell is provisioned.

The cell having been fully provisioned it is sealed with a mud plug of an even thickness of approximately 1 mm. Work then starts on the second cell. After the full number of cells has been completed the nest entrance is sealed with a mud plug leaving a vestibular cell. The distal opening of the turret is also sealed and the length of the turret may be subdivided by the construction of partitions. The final closure and the closure of the turret are very little thicker than the cell closures.

Life history

Egg hatch to full grown larva was observed in one instance only. The time taken was 9 days.

When a larva has consumed all its provision, it lines the cell with a parchment-like substance composed of "varnished" spinnings so firmly attached to the cell walls and the sealing plug that it cannot be removed without a coating of earth.

Female sleeping and sheltering habits during nesting

One instance of sheltering was observed on an overcast day. A female facing outwards was sheltering in a turret which was furnished with a seal at its inner end.

Associated insects

Four *Chrysis laminata* Mocsáry (as *Octochrysis laminata* in Gess, 1981) (Chrysididae) and one male *Anthrax ?tetraspilus* (Hesse) (Bombyliidae) were reared from cells of *T. guerinii* from the sandbank at Hilton.

DISCUSSION

In order to place the present ethological studies in context it seems useful to give a brief review of the published ethological accounts for the five genera here represented.

Nothing appears previously to have been published concerning the nesting of those species consigned by Giordani Soika (1987) to his new genus *Allepipona*. The present study of the ethology of *A. erythrospila* does not indicate any unique features but rather shows it to be of the general pattern exhibited by many eumenids excavating their nests in horizontally presented clayey soils.

The only previously published accounts of the nesting of *Antepipona* species are those of Roubaud (1916) and of Bonelli (1973a). Roubaud's study concerned the nesting of a species identified by him as *Odynerus tropicalis* Saussure (= *Antepipona tropicalis* (Saussure)) in Dahomey (Benin according to Giordani Soika (1985)). Whereas Giordani Soika (1985: 120) accepts Roubaud's species as belonging to *Antepipona* he points out that *tropicalis* does not occur in that part of west Africa and suggests that the species is more likely to have been *mucronata* (Saussure) or *fervida* (Saussure). Bonelli's studies concern the nesting in Ethiopia of *A. silaos* (Saussure) and of its subspecies *A. s. quartinae* (Gribodo) (as *A. asmarensis* (Schulthess)) (for synonymy see Giordani Soika, 1985: 91).

A. silaos is one of the commonest species of *Antepipona* and is widespread over the whole of central, eastern and southern Africa (Giordani Soika, 1961: 448 and 1985: 91) and is known also from the Grahamstown district where it is sympatric with *A. scutellaris*.

The nesting behaviour of *A. silaos* appears to be similar to that of *A. scutellaris*. The form of the underground workings and of the nest turret figured by Bonelli show no apparent significant differences except that only single-celled nests are recorded. *A. siloas* is recorded as making a final closure of the shaft using pieces of turret and then soil from around the entrance, water being used to moisten the soil to make a plug. This facet of behaviour was not recorded in the present study but it is likely that *A. scutellaris* also constructs a final closure.

The account of the nesting of Roubaud's *A. "tropicalis"* as rendered by Bequaert (1919: 185–186) shows that this species differs from *A. silaos* and *A. scutellaris* in that it excavates its burrows in clay walls (that is in a vertically rather than a horizontally presented substrate) though like the latter two species it furnishes the nest with an entrance turret. This turret is removed when the nest is closed. Possibly the materials of the turret are used for nest closure as are those of the turret of *A. silaos*. The nest galleries are short; as a rule bifurcate, each of the branches containing one, rarely two cells. *A. "tropicalis"* differs most markedly in apparently being a progressive provisioner and moreover in tending to care for more than one nest and more than one larva at a time.

Whereas the nesting behaviour of *Antepipona* species as judged from the studies of *A. silaos* and *A. scutellaris* appears to be both interspecifically uniform and unremarkable, the study of *A. "tropicalis"* suggests that considerable variation may occur within the genus as a whole.

The genus *Euodynerus* has a wide distribution, being represented in both the Old and the New worlds. Krombein (1979: 1491–1497) has indicated the diversity of the nesting habits known for the genus in North America and has briefly given the essential details of the nest form of individual species. A few North American species construct mud nests on rocks and a few species such as *E. annulatus* (Say) nest in clayey soils, the excavated vertical burrow being surmounted by a curved mud turret. The majority of species, however, nest in pre-existing cavities, principally in plant stems. Eight of these species, nesting in trap-nests, were studied by Krombein (1967: 56–85). In all these species the nest architecture appears to be very similar. Whereas cell partitions and closing plugs are always constructed of mud or agglutinated sand and nesting cavities appear never to be furnished with mud entrance turrets, the presence or absence

of preliminary plugs, intercalary cells and vestibular cells appears to be a variable character even intraspecifically.

The nesting of *E. euryspilus* is therefore typical of that of the *Euodynerus* species which nest in pre-existing cavities in plant stems.

The only published accounts of the nesting of *Rhynchium* seem to be a brief account of the nesting of *R. marginellum* in abandoned nesting burrows of *Xylocopa* (Anthophoridae) in Ethiopia (Bonelli, 1973b) and three accounts for *Rynchium oculatum* Spinola, a note on nesting in rose canes in southern France (Lichtenstein, 1869), a short account of nesting in reeds used in the construction of a wall in Italy (Grandi, 1961) and a fuller account of nesting in trap-nests in Egypt (Krombein, 1969). Nest construction in all cases seems to be similar to that of *R. m. sabulosum*. Empty intercalary and vestibular cells seem to be a common feature. Pyralidids are recorded as being used for provisioning by both species and noctuids in addition by *R. oculatum*.

As far as the authors can ascertain there is no published account of the nesting of any species of *Tricarinodynerus*. A photograph of *T. guerinii* (as *Odynerus* sp.) on its entrance turret has been reproduced in *Skaife's African Insect Life* (Revised edition, 1979: Plate 133) but it is not accompanied by a nesting account. The nests described from Hilton, Grahamstown in the present paper were all in relatively short cavities which only allowed the construction of a small number of cells. However, nests from False Bay, St Lucia in cut reeds, used in building construction, with cut open hollow internodes of up to 150 mm in length were constituted of up to 23 cells (Weaving, pers. comm.). *T. guerinii*, making use as it does of cavities in vertical earth banks, in "sandstone" banks, in shale cliffs, and in plant tissue, and of empty cells of wasps building aerial mud nests, shows considerable flexibility in its choice of nesting substrate unlike many nesters in pre-existing cavities which seem to be more restricted. *E. euryspilus* and *R. m. sabulosum* have for example not been found nesting in any substrate other than plant tissue.

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Parasites, generalist and specialist predators and their role in limiting the population size of blackflies and in particular *Simulium chutteri* Lewis (Diptera: Simuliidae) in and along the Vaal River, South Africa.

by

F. C. DE MOOR

(Albany Museum, Grahamstown)

ABSTRACT

Mermithid and microsporidial parasites found in simuliid larvae were monitored at weekly intervals during one year of a three and a half year study on the biology and ecology of Simuliidae in the Vaal River near Warrenton. Predators and their feeding behaviour on all life cycle stages of Simuliidae were recorded over the entire three and a half year period in and along the river. Several species of vertebrates and invertebrates were recorded as simuliid predators for the first time. Opportunistic predatory behaviour was observed in most vertebrate and the majority of invertebrate species identified in the study. Specialist predatory behaviour was observed in some Trichoptera species. An assessment is made of the role these various predator species play in limiting the population size of *Simulium chutteri* Lewis, a bloodsucking livestock pest in the region. The larval stages of two species of hydropsychid Trichoptera, *Cheumatopsyche thomasseti* (Ulmer) and *Amphipsyche scottae* Kimmins, were found sharing the stones-in-current biotope with the pest simuliid larvae and pupae. Population sizes of the two trichopteran species closely follow population size fluctuations of *S. chutteri*. These trichopterans contributed significantly to simuliid reduction at certain times of the year.

Observations made subsequently in and along other river systems and streams have revealed further instances of predation on larval and adult stages of Simuliidae. Examination of the gut contents of *Chiloglanis* species (mochokid rock catlets) sharing the stones-in-current biotope with several species of Simuliidae in rivers in the eastern Transvaal revealed possible specialist vertebrate predators of larval and pupal blackflies in Africa.

INTRODUCTION

Aquatic Mermithidae (Nematoda) that attack simuliid larvae have long been considered as potential biological control agents (Poinar 1981). Crosskey (1990) records 67 species in five genera of mermithids which have been collected from blackfly hosts. Infection rates of up to 68% have been recorded in populations of simuliid larvae but a rate of between 1-10% is perhaps more commonly encountered (see references in Crosskey 1990). The taxonomy and culturing techniques for developing suitable numbers of desired specific mermithid parasites are not well enough understood at present to enable isolation and large scale breeding of suitable species (Finney 1981). About 30 species of Microsporidia representing six families of Microspora (Protozoa) are so far known to be parasitic on simuliid larvae. Recorded rates of infection by Microsporidia in nature are usually below 1% but are occasionally above 15% (Crosskey 1990). Microsporidia, although used successfully to control mosquito colonies (Alger and Undeen 1970), have so far not been used for blackfly control.

Predators of both the aquatic and non-aquatic stages of Simuliidae have been well documented. In a recent review Davies (1981) records 206 species of invertebrates and 96 species of vertebrates as predators of blackfly larvae, pupae, adults and eggs. Direct observation of predation and the examination of gut contents of potential predators for prey remains are the most frequently used techniques. More recently the serological study of smears of gut contents of potential predators to identify protein remains of *Simulium damnosum sensu lato* Theobald have been used (Service and Lyle 1975, Service and Elouard 1980). A note of caution should be added as both predation and scavenging would be revealed using this last technique.

The influence predators have on the population size of blackflies has been estimated from minimal to very significant. Davies (1981) states that Speir (1976) estimated that predation accounted for 82.6% of larval simuliid mortality in western Oregon streams (USA). Some of the most revealing studies on the importance of predators in controlling blackfly population size were reported by Hynes and Williams (1962) and Ide (1967) who found that insecticidal control of simuliids also led to a decline in their natural trichopteran and plecopteran predators. Because of their slow rate of recovery the numbers of these predators remained low in subsequent years whereas increased numbers of blackflies were observed in years following insecticidal treatment of streams.

In most instances it has only been possible to determine predators without assessing their importance as population size regulators of Simuliidae (Crosskey 1990). Some recent studies (Merritt and Wotton 1988, Wotton and Merritt 1988) attempted to evaluate predation on blackflies in a quantitative way. A three and a half year study of a community of benthic invertebrates in stones-in-current biotopes in the Vaal River near Warrenton (de Moor 1982a) and subsequent observations and discussions with colleagues have provided some insight into the impact of parasitism and predation on simuliid populations.

METHODS

Between June 1977 and March 1981 a study on the ecology, biology and population fluctuations of Simuliidae in and along the Vaal River near Warrenton was undertaken (de Moor 1982a). This study included a one year assessment of parasites in simuliid larvae. Predators of Simuliidae were recorded and the possible impact on limiting the population size and growth rate of *S. chutteri* were studied over the whole three and a half year period. Observations of predatory activity were recorded. Where possible photographic records were made, specimens of predators were collected, gut contents of suspected predators were examined, and identified predatory invertebrates were sent to specialists for verification.

In order to estimate population sizes of benthic simuliids and associated fauna monthly samples of natural substrates were collected from the stones-in-current biotope from rapids in the Vaal River on the Farm Witrand between July 1978 and March 1981. In addition, samples of animals drifting in the flowing water column were collected at regular intervals during this period using Cushing-Mundie or Paddle-wheel drift samplers (de Moor 1982a, de Moor, Chutter and de Moor 1986). For an assessment of parasites weekly samples of simuliid larvae and pupae were collected from artificial substrates for one year (de Moor 1982a).

As the distribution of benthic animals on substrates at any one date was in most instances found to be contagious (*sensu* Elliott 1977) it did not allow for the expression of population estimates using standard arithmetical mean values. After $\log_e$ transformation it was found that the majority of data sets conformed to a normal distribution. From Sichel (1966) an estimate of the average count, given by the maximum likelihood estimator for the mean of a lognormal population was determined and is referred to as the Sichel mean (de Moor 1982a). All data sets presented give population size

estimates as Sichel mean counts.

Voucher specimens of the predators observed and collected are housed in the National Museum, Bulawayo (Odonata); British Museum of Natural History, London (Diptera); Plant Protection Research Institute, Pretoria (Arachnida); and Albany Museum, Grahamstown (Diptera, Trichoptera, Plecoptera). Parasites of simuliid larvae were not identified to generic level. They are preserved together with their hosts in the Albany Museum, Grahamstown.

OBSERVATIONS OF PARASITES IN SIMULIIDAE

Two kinds of parasites, mermithid nematodes and microsporidial protozoans were identified from Simuliidae collected in the Vaal River. A decrease in the percentage of *S. chutteri* pupae as a total of all Simuliidae and an increase in mermithid parasitism found by Chutter (1968) was not discernible in the data gathered over a year from the Vaal River (Fig. 1). The highest percentage of mermithid parasitized *S. chutteri* larvae were found between August and October 1979 when simuliid population levels were increasing (see Figs 6, 7 and 8) and when *S. chutteri* pupae, expressed as a percentage of all Simuliidae (to make this data set comparable with Chutter's (1968) study), were also increasing (Fig. 1). The observed decrease of pupal numbers in September 1979 was because vandals had removed all the rods with artificial substrates from the river between 31 August and 6 September (this is indicated by the arrow in Fig. 1). This disturbance prevented data from being gathered during this week and it took a further three weeks before the simuliid population on

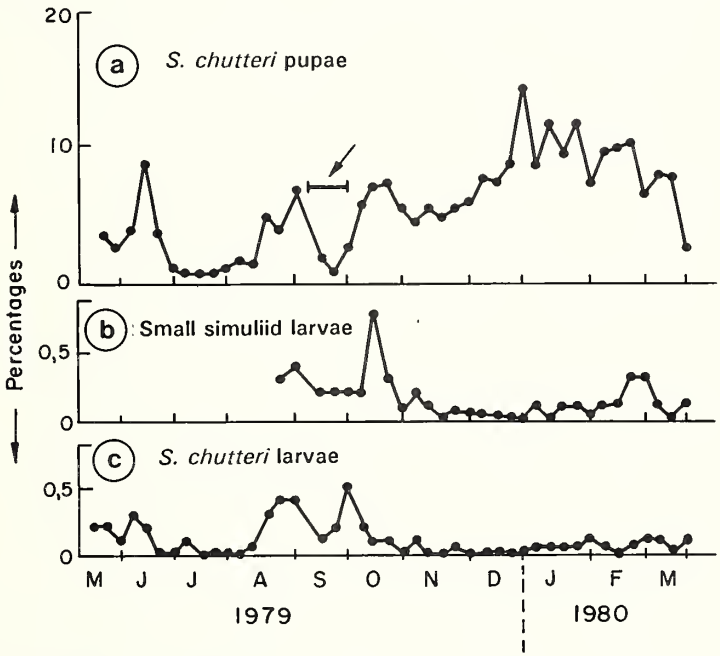

Fig. 1.a) *Simulium chutteri* pupae as a percentage of the total number of Simuliidae. b) The percentage of small simuliid larvae parasitised by Mermithidae. c) The percentage of *S. chutteri* larvae parasitised by Mermithidae. Samples of Simuliidae examined were collected from artificial substrates at weekly intervals from 10 March 1979 to 20 March 1980.

artificial substrates again attained a level comparable to the natural population. It should be noted that there are natural seasonal fluctuations in population sizes of simuliid larvae and pupae (de Moor 1982a) and that, when pupae are expressed as a percentage of the total Simuliidae, the role parasitism by Mermithidae plays in controlling pupal numbers may be erroneously correlated. The discovery by Mr G.J. Begemann in September 1977 (pers. comm.) of a live mermithid worm in an adult female *S. chutteri* indicated that infestation of *S. chutteri* larvae by Mermithidae did not necessarily prevent pupation, confirming Anderson and Dicke's (1960) observation on North American species. Reproduction would, however, be prevented because the ovaries of this female were atrophied.

The percentage of parasitism in Simuliidae observed by Carlsson (1967) increased markedly above certain minimum population densities. The population density of *S. chutteri* in 1979 and 1980 was apparently low enough to prevent intense parasitism by Mermithidae and observed parasitism remained below 1% throughout that period (Fig. 1b and c). This indicated that parasitism played a minor role in controlling the population size of *S. chutteri*.

It should be noted that parasitism by Nematodes was only discernible when large worms were seen in the gut and body cavity of *Simulium* larvae. Many larvae infested by small mermithids, as well as those that may have perished due to mermithid parasitism may have been missed in the survey. By standardizing the technique by only recording observed parasites, results are comparable throughout the period of the study.

Simulium adersi Pomeroy was also parasitized by Mermithidae as well as by Microsporidia (Fig. 2). The percentage of larvae parasitized by Mermithidae was below 2% for the entire period (Fig. 2b) but was noticeably higher when the population size of *S. adersi* larvae was higher (Fig. 2a). Mermithidae thus appear to have played a more significant role in controlling the population size of

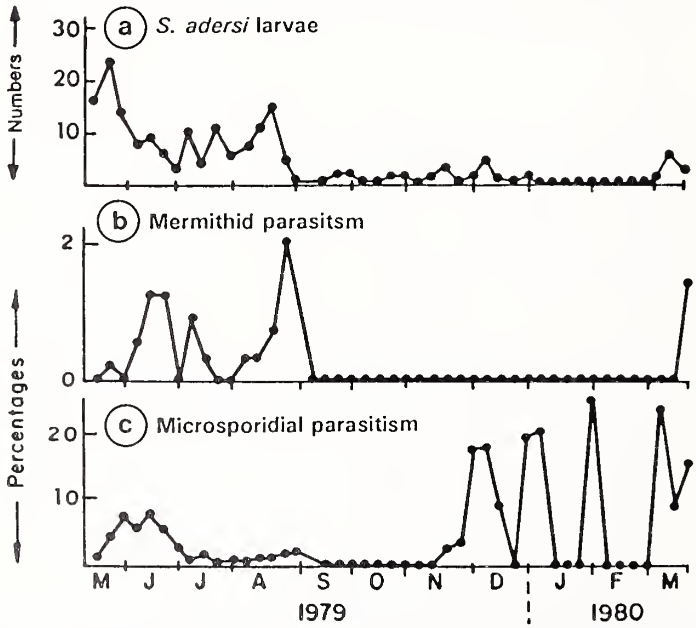

Fig. 2.a) Sichel mean numbers of large *Simulium adersi* larvae on artificial substrates. b) Percentage of *S. adersi* larvae parasitised by Mermithidae. c) Percentage of *S. adersi* larvae parasitised by Microsporidia. Artificial substrates collected at weekly intervals from 10 March 1979 to 20 March 1980.

S. adersi than that of *S. chutteri*. Parasitism by Microsporidia was recorded in up to 24% of large larvae (Fig. 2c). High parasitism by Microsporidia may have caused the observed decline of the larval *S. adersi* population in June 1979 and may also have caused the low number of *S. adersi* observed from November 1979 through to March 1980 (Fig. 2a). Although not entirely temporally separated infestations by Microsporidia were highest during the summer months whereas Mermithidae were more prevalent in the cooler autumn through to spring.

TABLE 1. Predators of Simuliidae collected or observed, and identified in a three and a half year study along the Vaal River near Warrenton.

SPECIES	FEEDING ON	IDENTIFIED BY
Osteichthyes		
Clarias gariepinus (Burchell)	Larvae, pupae and adult Simuliidae#*	F C de Moor
Aves		
Motacilla flava Lin.	Picking adults off reeds#	F C & I J de Moor
Zosterops pallidus Swainson	Picking adults off reeds#	F C & I J de Moor
Cossypha caffra (Lin.)	Picking adults off reeds#	F C & I J de Moor
Motacilla capensis Lin. *Turdus olivaceus* Lin. *Ploceus velatus* Vieillot	Picking adults off water surface while standing on emerging stones in water#	F C & I J de Moor
Hirundo spilodera (Sundevall) *Riparia paludicola* (Vieillot)	Catching adults in flight (Hawking)#	F C & I J de Moor
Hirudinoidea		
Salifa perspicax Blanchard	simuliid larvae*	F C de Moor
Crustacea: Decapoda		
Potamonautes warreni Calman	simuliid larvae & pupae#*	F C de Moor
Arachnida		
Larinia sp	Adult Simuliidae#	A S Dippenaar
Tetragnatha andonea Lawrence	Adult Simuliidae#	A S Dippenaar
Insecta:		
Plecoptera		
Neoperla spio s.l. (Newman)	simuliid larvae*	M Picker**
Odonata	Adult Simuliidae#	E C G Pinhey (see Table 2)
Diptera		
Limnophora bella Pont	Pupae and adult Simuliidae#	A Pont
Wiedemannia sp.	Adult Simuliidae#	B R Stuckenberg
Trichoptera		
Ecnomus thomasseti Mosely	simuliid larvae*	K M F Scott
Cheumatopsyche thomasseti (Ulmer)	simuliid larvae*	K M F Scott
Amphipsyche scottae Kimmins	simuliid larvae and eggs*	K M F Scott

\# Animals observed feeding on Simuliidae
* Simuliid remains identified from gut contents
** Identified as two different species from eggs found in numphs

It was apparent that *S. adersi*, even though present in the rapids at Witrand in lower numbers than *S. chutteri* during 1979 and 1980, was more severely infested by parasites, both Mermithidae and Microsporidia, than was that species. This could be due to *S. adersi* occupying a biotope not optimally suited to the average individuals of that species. A broadening of this species' niche would then lead to reduced fitness, and hence greater susceptibility to parasitism, in individuals found occupying marginal regions of their extended biotope (de Moor 1982a).

As parasites in the study on the Vaal River were found not to have a noticeably significant impact on simuliid populations they will not be further discussed in this paper.

OBSERVATIONS AND EXAMINATION OF PREDATORS OF SIMULIIDAE

During the course of the three and a half year study a number of vertebrates and invertebrates were observed feeding, identified as feeding from gut content analysis and associated with feeding on blackflies because of their activity and abundance around the rapids on the Vaal River where the study was conducted (Tables 1 and 2). Each group of animals is described and details of observations are recorded.

Osteichthyes

In September and October 1977, October 1978 and August 1980 when simuliid pupal numbers were high (see Fig. 6) and adult simuliids were emerging and actively flying around rapids, large (up to c 800 mm long) sharp toothed catfish *Clarias gariepinus* (Burchell) were noted to be conducting a combination of surface and formation feeding (Bruton 1979) in large pools below rapids. On each occasion numbers of fish were observed to swim in evenly-spaced regular formation, forming a semi-circular front line with individuals in the centre further back than those on the extreme ends. More individuals were staggered behind the leaders. They swam slowly towards the bottom end of rapids, the origin of the food source, with their bodies nearly parallel to the water surface and their mouths open with barbels extended along the surface of the water, thus guiding into their mouths material drifting on or just below the surface. They periodically closed their mouths, dived below the surface and then surfaced again, continuing the activity. This type of feeding concentrates the food source and maximizes food gathering effort. Fish behind the leaders scooped up any food items not gathered (Fig. 3).

Close examination of the water surface confirmed that there were large numbers of adult Simuliidae caught in patches of scum. The examination of gut contents of *C. gariepinus* collected below the rapids, conducted on several occasions, revealed that mostly adult but also larval and pupal simuliids comprised numerically the major food source. One fish colleeted in October 1977 had in its stomach a crab *Potamonautes warreni* Calman, three mayfly nymphs, two *Baetis glaucus* Agnew and one *Choroterpes ? elegans* (Barnard), two chironomid larvae and 57 larvae of *Simulium* spp., predominantly *S. chutteri*. In October 1978 another fish stomach contained one *P. warreni*, two anthomyid pupae, one tipulid pupa, one hydroptilid trichopteran (*Catoxyethira* sp.) pupal case, three larvae, nine pupae and 641 adults of *S. chutteri*. In addition some adult terrestrial insects which had accidentally fallen into the water had been taken and included beetles (five Rutelinae, one Chrysomelidae and one Carabidae) and bugs (two Lygaeidae and one Aphidae). The gut contents of a third fish was composed almost entirely of *S. chutteri*, several thousand pupae and a few adults. This would suggest that the fish had actually scraped pupae off stones in and below the rapids. Bruton (1979) records that *C. gariepinus* feeds most frequently on abundant and easily accessible prey

animals and that invertebrates are numerically the most important food item in their diet. In times of shortage of a particular prey animal *C. gariepinus* readily switches to other more easily obtainable food sources. The almost exclusive feeding on simuliid pupae by one individual of *C. gariepinus* confirms an innovative opportunistic feeding strategy.

Stomach content analysis of *Barbus aeneus* (Burchell) during the study on the Vaal River did not reveal any feeding on Simuliidae. In a study of feeding behaviour of *Oreochromis mossambicus* (Peters) it was found that the juveniles of this predominantly detritivorous or herbivorous fish species fed almost exclusively on benthic insect larvae during an early phase of their life (de Moor, Wilkinson and Herbst 1986). For this reason juveniles of large herbivorous fish species in the Vaal River should also be considered as potential predators of Simuliidae.

Observations and studies subsequent to the research conducted on the Vaal River have identified other fish species as predators of Simuliidae. Analysis of the stomach contents of the mochokid rock catlet, *Chiloglanis pretoriae* van der Horst (undertaken for P. de Villiers by H. M. Barber) confirmed that this species feeds almost exclusively on aquatic insects found in riffle or stones-in-current biotopes. Orthoclad chironomid as well as simuliid larvae formed a significant component of the stomach contents of the mochokid rock catlets investigated. *Chiloglanis pretoriae* is found in rapids and riffles with water flow ranging between 0,8 - 1,0 ms^{-1} in tropical and sub-tropical rivers in southern Africa (de Villiers 1991). Miss S. Pollard (pers. comm.) also confirms that *Chiloglanis anoterus* Crass feeds on orthoclad chironomid larvae indicating that this species too confines its feeding activity to swift running water biotopes. Another species *Chiloglanis paratus* Crass was collected by the author in the swiftest of currents on bare bedrock in the lower reaches of the Sabie River in the Kruger National Park in October 1990. The correspondingly low density of simuliid larvae in this and other rivers in the eastern Transvaal at this time of the year,

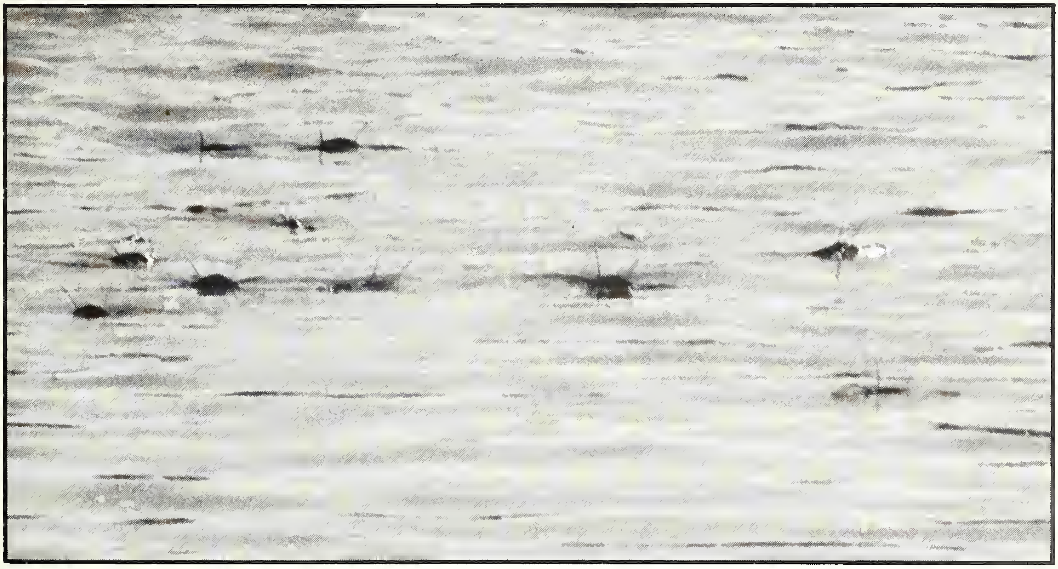

Fig. 3. A formation of sharp toothed catfish *Clarias gariepinus* feeding on the water surface in the Vaal River downstream of large rapids on the farm Witrand.

when one might expect high densities of simuliid larvae and pupae, could possibly be construed as being a result of the abundance of these small mochokid fish. These fish would very successfully remove sedentary simuliid larvae and pupae from substrates in the swiftest of rapids. To verify this hypothesis a detailed study on the life history of simuliid species and their predators in the rivers of the Kruger National Park would have to be undertaken.

Aves

Birds were often seen feeding on blackflies when large numbers of adult *S. chutteri* were observed during the spring in all three years of the study on the Vaal River (Table 1). Certain species picked floating adults off the water surface while perched on exposed stones in and below rapids, while others were observed actively searching among reeds while perched on their stems along the banks of the river. It was recorded that large numbers, mostly of male adult *S. chutteri*, settled on reeds and sedges along the river banks at this time of the year. Swallows and martins were often observed hawking, catching adult flies in flight, when there were swarms of male *S. chutteri* flying above and around rapids (Fig. 4). They also hawked above reeds lining the banks of the river. Each year between August and December swallows and martins were most active around rapids harbouring large populations of simuliids. In June 1977 when abundant adult simuliid activity was still observed African Sand Martins *Riparia paludicola* (Vieillot) were observed hawking above the rapids in the Vaal River on the farm Witrand.

Fig. 4. Dense swarm of adult male *Simulium chutteri* flying above rapids on the Orange River below Marksdrift Weir.

Hirudinoidea

The predatory freshwater leech *Salifa perspicax* Blanchard was identified as a predator of Simuliidae by Chutter (1968). Gut content analysis of two specimens collected by the author in December 1980 revealed respectively eight and 16 whole simuliid larvae ranging from fourth to final instars. This confirms that *S. perspicax* is a voracious predator of simuliid larvae. This leech was found co-existing with simuliids in the stones-in-current biotope in June 1977, August 1979, October and December 1980.

Crustacea

Davies (1981) records species of four families of Crustacea, including two species of Potamonidae *Potamonautes niloticus* (H. Milne-Edwards) and *P. berardi* (Audouin), as predators of Simuliidae. In the present study, from 30 November to 3 December 1980, when the level of the Vaal River was low and the flow in the normally swift rapids was reduced to a trickle, medium sized *Potamonautes warreni* Calman (carapace width 50-70 mm) were observed amongst the stones where sampling was regularly conducted. On closer examination they were seen to scrape their chelae along the submerged stone surface and go through feeding motions. A crab was collected and preserved in formalin. Examination of the gut contents of this crab, although very finely masticated, confirmed that it had been feeding on simuliid larvae and pupae. Regurgitated, un-masticated gut contents contained 88 large *S. chutteri* larvae and 78 smaller simuliid and ten orthocladiine chironomid larvae.

Arachnida

Web spinning spiders were frequently observed with simuliid adult remains. Webs were spun amongst vegetation bordering the river banks, between large boulders and stones, and occasionally on drift sampling apparatus left near rapids. Spiders were observed to be most active when adult simuliids were abundant between August and February. Two species were identified in the present study (Table 1).

Insecta

Plecoptera

Stoneflies identified as *Neoperla spio sensu lato* (Newman) but belonging to a species complex (Picker 1980) were found to be one of the most voracious aquatic invertebrate predators in the present study. They were encountered in the same biotope as simuliid larvae and pupae in August and September 1977, July and November 1978, January, March, November and December 1979, January, March, July, November and December 1980, January and March 1981. Large nymphs, final instar nymphal shucks and adults were observed from November through to March each year. Nymphs of *N. spio* encountered in July, August and September were at an earlier stage of development. Gut content analysis of a number of nymphs revealed that they fed on fourth to final instar larvae of Simuliidae as well as small to large larvae of *Cheumatopsyche thomasseti* (Trichoptera), and nymphs of *Baetis glaucus* and *Afronurus* sp. (Ephemeroptera).

Odonata

Crisp (1956) found that only 7 percent of adult Odonata collected over a two week period had taken simuliid adults. They could therefore not be considered to be very important predators. Although the nymphal stages of Odonata are recognised as voracious predators on all forms of aquatic animals they were never encountered in the same biotope as the simuliid larvae collected in the present study. Adult Odonata were often observed hawking amongst swarms of adult simuliids around rapids from October to April. As all adult Odonata are known predators of a number of flying insects a collection of these was made (Table 2). It should be noted that dates when Odonata were collected were not the only times when they were present. Smaller species belonging principally to the Zygoptera, in particular *Ischnura senegalensis* (Rambur) which was present throughout the summer period, are potentially more efficient predators of adult simuliids than some of the larger Libellulidae belonging to the Anisoptera. *Ischnura senegalensis* was the most abundant dragonfly and would, because of its smaller size, have to expend less energy to obtain sufficient food from capturing adult simuliids than would the larger Anisoptera.

TABLE 2. Adult Odonata collected alongside rapids on the Vaal River on the farm Witrand from 1977 to 1980. Months when collected indicated. Species identified by E C G Pinhey.

SPECIES	MONTH AND YEAR COLLECTED
Platycnemididae	
Mesocnemis singularis Karsch	Dec 1979
Protoneuridae	
Elattoneura glauca (Selys)	Oct, Nov, Dec 1977; Oct 1978; Dec 1980
Chlorocyphidae	
Platycypha caligata (Selys)	Jan 1980
Coenagrionidae	
Pseudagrion salisburyense Ris	Oct 1977; Oct, Nov 1978; Jan 1980
P. vaalense Chutter	Oct, Nov 1977; Oct 1978
P. massaicum Sjöstedt	Nov 1977
Ischnura senegalensis (Rambur)	Nov 1977
Gomphidae	
Crenigomphus hartmanni (Förster)	Jan 1980
Corduliidae	
Macromia picta Selys	Nov 1977
Libellulidae	
Orthetrum caffrum (Burmeister)	Oct, Nov 1977
O. abbotti Calvert	Mar 1979
O. chrysostigma (Burmeister)	Oct 1978; Jan 1980
Sympetrum fonscolombei (Selys)	Nov 1977
Trithemis furva Karsch	Nov, Dec 1977; Apr 1979; Jan 1980
T. kirbyi ardens Gerstaecker	Mar 1979; Jan 1980
Palpopleura jucunda Rambur	Mar 1978
Crocothemis servilia erythraea (Brullé)	Oct 1978
C. sanguinolenta (Burmeister)	Jan 1980
Diplacodes lefebvrei (Rambur)	Oct 1978

Coleoptera

Crosskey (1990) notes that several families of aquatic beetles have been recorded as feeding on simuliids. He suggests, because of their close association in the swift water biotope, that adult elmids regularly prey on Simuliidae and adds that serological tests have verified this. In the present study both larvae and adults of several species of elmid beetles were collected in the same biotope as simuliid larvae and pupae. They were encountered in 12 of the 32 monthly samples collected. Predation by Elmidae was not, however, confirmed.

No actual observations of predation on Simuliidae by any Coleoptera were made in the present study. Larvae of a gyrinid, *Aulonogyrus* sp., were found coexisting with simuliids in the stones-in-current biotope during 21 of the 32 months. They were on occasion found running around amongst dense masses of simuliid larvae and pupae on stones collected from rapids. Gyrinid larvae kill their prey and inject digestive juices into them with their hollow sickle-shaped mandibles. They then imbibe the partially digested contents of their prey leaving the empty skin-cast behind. As serological determination of prey species of the *Aulonogyrus* sp. was not carried out in the present study predation on Simuliidae could not be confirmed.

Diptera

Crosskey (1990) states that among the Diptera, Simuliidae must be regarded as their own worst enemies as predation by larger simuliid larvae on smaller ones may be one of the most important predatory impacts on larval simuliid populations. Cannibalism is recorded in several species (Burton 1971, Chutter 1972, Disney 1972a) but an examination of the larval gut contents of 100 *S. chutteri* in the present study revealed no identifiable blackfly remains. Cannibalism in *S. chutteri* would be low because the various instar stages are found to concentrate in different regions of the river during their life cycle thus limiting contact between individuals at different developmental stages (de Moor, Chutter and de Moor 1986).

Adults of the muscid fly identified by Mr A. Pont as "very near or identical to *Limnophora bella* Pont" were observed on a number of occasions feeding on larval and adult simuliids. In September 1978 when the flow of the river had suddenly decreased and left many stones with simuliid larvae stranded in shallow trickles of water and pupae exposed to the air, adult *L. bella* were observed flying around pupae and settling on them. They attacked pupae in their cocoons and pulled out partially emerged adult simuliids and started feeding on them. It was also noted that male *S. chutteri* were also hovering around pupae apparently waiting for females to emerge so that they could commence mating. In November 1978, when metal rods with attached artificial substrates were removed from the water and left exposed while substrate samples were collected for study purposes, it was noted that a large number of simuliid larvae and pupae had colonised the metal rods. Adult *L. bella* were observed walking along these rods catching and eating larvae. They also settled on exposed stones just above the splash zone and searched for emerging adult simuliids which they attacked on the surface of the water. In addition they were observed on stones around rapids in September 1977, January 1980 and February 1981.

In October 1979 a number of individuals belonging to another species of fly (identified, from a female collected, as an empidid, *Wiedemannia* sp.) were observed catching adult simuliids in flight and devouring them while settled on stones (Fig. 5). In February 1980 individuals of this species were again observed feeding on adult simuliids.

Fig. 5. An empidid fly *Wiedemannia* sp., settled on a boulder, feeding on a newly emerged simuliid fly.

Trichoptera

Although all the above recorded invertebrate predators of Simuliidae played some role in controlling simuliid population sizes they were all found in low densities compared to the simuliids. Some of the trichopteran predators discussed below, however, appeared in sufficiently large numbers to have an effective impact on simuliid numbers at certain times of the year. Hydropsychid Trichoptera, because they closely share the same substrates with many simuliid species, are documented as efficient predators of Simuliidae in many countries (see Davies 1981). The impact of certain species of predatory caddis on simuliid population size has been briefly discussed by the author before (de Moor in press) and is considered in greater detail here.

The mouthparts of the larvae of *Orthotrichia* species belonging to the microcaddis family Hydroptilidae are modified for piercing enabling them to get at the cytoplasmic contents of algal cells on which they normally feed. An *Orthotrichia* species was, however, observed feeding on simuliid pupae by Burton and McCrae (1972) who suggested that large numbers of this hydroptilid could cause considerable pupal mortality in simuliids. Disney (1972b) recorded the larvae of a species of *Orthotrichia* feeding on simuliid pupae and eggs. No direct observation of any *Orthotrichia* species larvae feeding on simuliid pupae was made in the present study. Total numbers of hydroptilid larvae (comprising almost entirely an *Orthotrichia* species), found on the same substrates as simuliid pupae in 31 of the 32 monthly samples collected, reached peaks in November each year and in January

1981. This coincided with a noticeable decrease in numbers of simuliid pupae in subsequent months (Fig. 6).

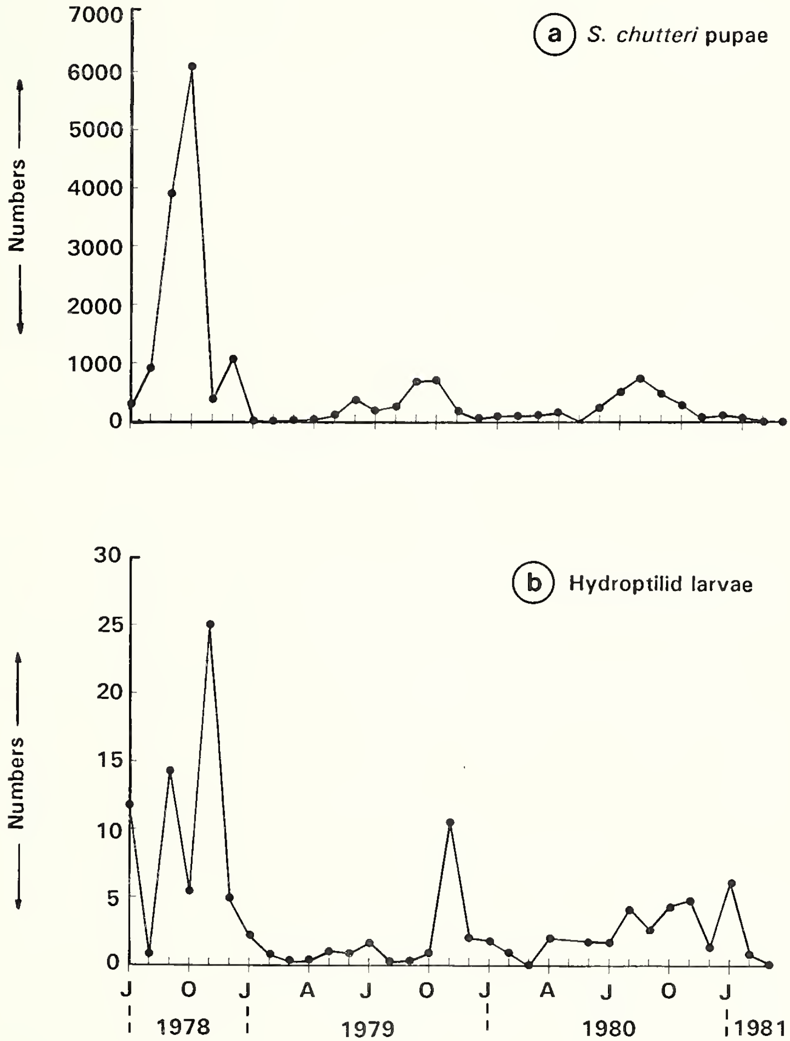

Fig. 6. Numbers of a) *Simulium chutteri* pupae and b) Hydroptilidae larvae collected from natural stones-in-current substrates at monthly intervals between July 1978 and March 1981. Counts expressed as Sichel mean numbers per 1000 cm² of stone surface area.

The net spinning Hydropsychidae capture food by means of a silk spun net suspended in the current from their retreat structure. They periodically move out of their shelter and remove any food items which have become entangled in the net. Two species of larval hydropsychids, *Amphipsyche scottae* Kimmins and *Cheumatopsyche thomasseti* (Ulmer), and one species of ecnomid, *Ecnomus thomasseti* Mosely, were identified from stomach content analysis as predators of Simuliidae in the Vaal River near Warrenton. Predation by the two species of hydropsychid was recorded in the months of November, December, March and April of several years and that by the ecnomid in May and January. The examination of the gut contents of a range of different instars of *C. thomasseti* larvae revealed that this species became more carnivorous with increasing size (Table 3). This confirmed the findings of Wallace (1975) that small hydropsychid larvae tend to be plant and detritus feeders whereas larger larvae feed more on animal matter. It is thus clear that large *C. thomasseti* larvae would have a bigger impact as predators of simuliid larvae than small ones. Third to fifth instar simuliid larval remains were most commonly found in the foregut of medium to large *C. thomasseti* larvae.

TABLE 3. The number and percentage of *Cheumatopsyche thomasseti* (Ulmer) larvae feeding on simuliid larvae. Instar stage of caddis larvae determined from head capsule measurements made from the base of mandibles to posterior margin of postgena. Larvae collected on 12 November 1980.

Average head capsule size	Instar stage of larvae	Number of larvae examined	Larvae with simuliid remains in gut	Percentage of larvae feeding on
120	3	11	1	9
185	4	10	4	40
245	5	9	7	78

Larvae of *C. thomasseti* were found coexisting with simuliids in the stones-in-current biotope in all the 32 months that samples were collected and larvae of *A. scottae* were found in 28 months. Simuliidae (comprising 80% or more *S. chutteri* in all samples collected) were always the most abundant and hydropsychid larvae were either the second or third most abundant benthic macro-invertebrates co-existing in the natural stones-in-current biotope in the Vaal River. As *C. thomasseti* was the most numerous hydropsychid the discussion on the impact of predators on the simuliid population will concentrate on this species.

A decrease in the numbers of *C. thomasseti* larvae between July and September in each of the three years of the study coincided with an exponential increase of simuliid larvae in the stones-in-current biotope between August and October in 1978 and 1979 (Fig. 7). Samples of adult Hydropsychidae collected from swarms flying above large boulders along the banks of the Vaal River on the farm Witrand during September 1977, 1979 and 1980, consisted entirely of male *C. thomasseti*. This indicated that a large synchronous emergence of this species had occurred which suggests that males form mating swarms in spring. The increase of small hydropsychid larvae in drift samples from late September onwards (Fig. 8) and the appearance of large numbers of small hydropsychid larvae in the stones-in-current biotope in October each year and *C. thomasseti* larvae during November 1978 and 1979 and October 1980 (Fig. 7) confirmed that mating and recruitment had occurred. The observed increase in the size of the *C. thomasseti* population was followed by a decline in simuliid numbers during November in all three years of the study (Fig. 7). It was also notable that the size of the *C. thomasseti* population was considerably higher during years when population levels of Simuliidae were also high (Fig. 7).

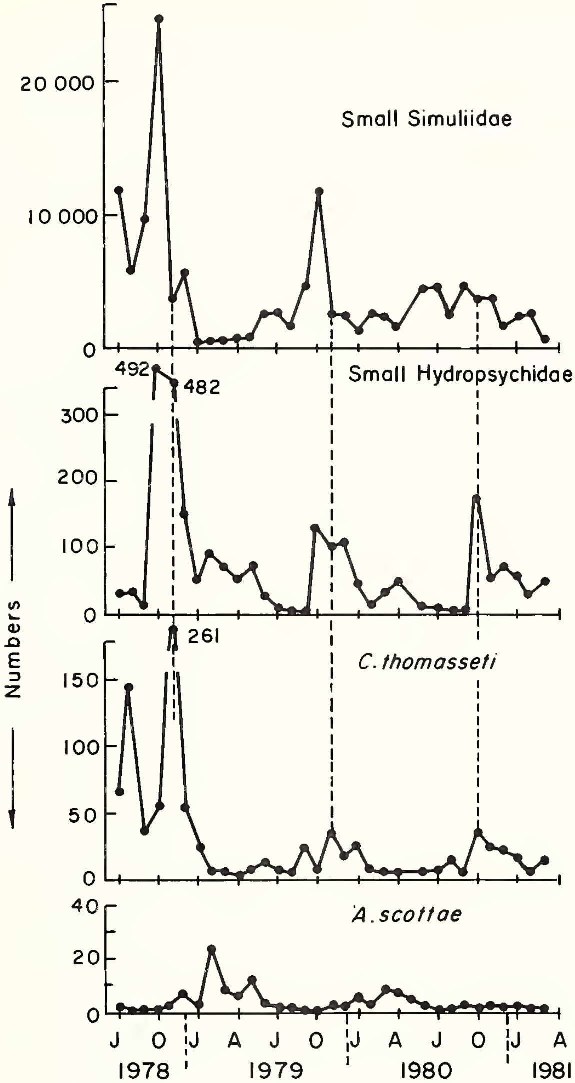

Fig. 7. Numbers of Simuliidae and Hydropsychidae larvae collected from natural stones-in-current substrates at monthly intervals between July 1978 and March 1981. Counts expressed as Sichel mean numbers per 1000 cm² of stone surface area.

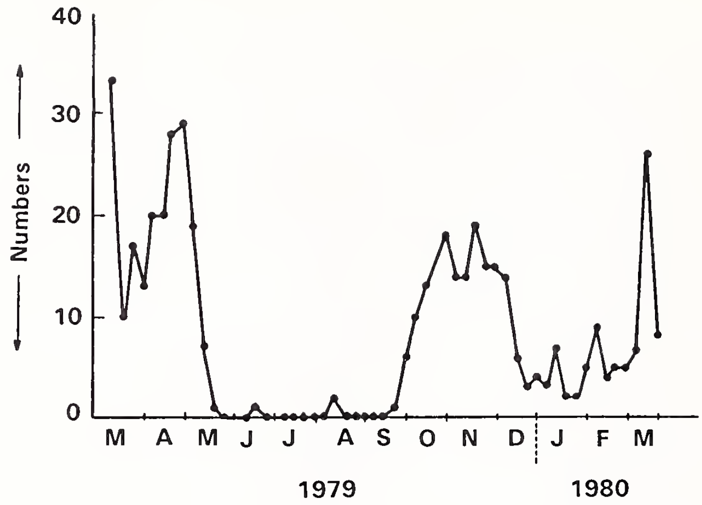

Fig. 8. The number of small hydropsychid larvae per 1000 litres of drifting river water collected upstream of rapids on the farm Witrand at weekly intervals between 10 March 1979 and 20 March 1980.

From December 1978 to May 1979 and from January to May 1980 there was an increase of *A. scottae* larvae (Fig. 7). Although the numbers of larvae of this species were lower than those of *C. thomasseti* in the preceding months the temporal separation of large larvae of these two species would allow for an extended period of predation on simuliids by hydropsychids.

The expected annual increase of simuliid larvae between August and October did not occur in 1980. This was because a successful waterflow regulation programme effectively kept in check the population growth of a large winter population of *S. chutteri*. The water flow regulation programme was carefully timed that year to ensure that it did not disrupt the breeding cycle and recruitment of *C. thomasseti* (de Moor 1982a, 1986).

The small larvae of *C. thomasseti* initially feed on detritus and algae but as they grow they require progressively more animal protein. Provided that the simuliid population size is not too large predation by large *C. thomasseti* larvae in November should halt any further exponential growth of the simuliid population. The effect a predator species can have on limiting the population size of a prey species is determined by the size of both the prey and predator populations. If the size of the prey population is disproportionately large the impact of the predators on the prey population will be negligible (Carlsson, Nilsson, Svensson, Ulfstrand and Wotton 1977).

Hymenoptera

Gess (1980) records the sphecid wasp *Dasyproctus westermanni* (Dahlbom) on the farm Hilton near Grahamstown in the eastern Cape as provisioning its nests with several families of Diptera including simuliid adults. Examination of 13 of these flies by the author revealed that four males and seven females were *Simulium adersi* Pomeroy and one female was identified as *Simulium nigritarse*

Coquillett. Five of the females had swollen abdomens revealing the remains of a blood meal. This would indicate that these flies were caught after taking a bloodmeal, probably while resting waiting to digest their bloodmeal and complete egg development. Digestion of blood takes three days or more and females resting on foliage would be vulnerable to searching predators such as sphecid wasps. Crosskey (1990) records several instances where wasp blackfly-predators wait around mammalian hosts, including man, and pick off female blackflies while they are engorging on their hosts.

In December 1985 on a field outing with F. W. Gess to Hilton the author was shown nests of *D. westermanni*. It appeared that the majority of flies they used for provisioning these nests were Simuliidae. Material was not collected and the simuliid species were not identified.

DISCUSSION

In the cooler temperate regions of the northern hemisphere, distinct seasonal breeding of many species of Simuliidae has been recorded and a succession of emergences of simuliid species occurs from spring through to autumn each year. In the Vaal River with a much warmer water temperature (de Moor 1982b) breeding and emergence of adults of various species occurs throughout the year. There are, however, distinct increases of various species at certain times of the year (de Moor 1986) and in the dominant species, *S. chutteri*, this usually occurred around September-October each year.

Crosskey (1990) notes that there are more recorded predators on the aquatic stages of blackflies than on adults. In the many studies conducted to control simuliid population size no real specialist predators have been found. It should be realised that predators in general are seldom restricted to one prey species. The simuliid predators discussed in the present paper can in the author's opinion, however, be placed into a continuum ranging from opportunistic to specialist predators.

The more specialist predators are species that for obvious reasons must temporally and spatially closely share the same biotope as their prey species. They must furthermore show some identifiable population fluctuations which tie in with fluctuations of their prey species. The hydropsychid Trichoptera clearly did show this. They were found on the same stones from which dense populations of *S. chutteri* were collected and their population sizes closely followed those of this species. They were less abundant when the simuliid population size was low during the same season in consecutive years (Fig. 7).

For controlling the population size of a rapids dwelling simuliid species such as *S. chutteri* a predatory caddis species such as *C. thomasseti* would be most effective. Although hydroptilid larvae of the genus *Orthotrichia* have been recorded as voracious predators of simuliid eggs and pupae (Burton and McCrae 1972, Disney 1972b) their low numbers found in association with the Simuliidae on stone substrates in the present study would suggest that they probably play a minimal role in their control.

During the study on the Vaal River water flow was periodically regulated to study the effect this would have on the simuliid population size (de Moor 1982a). Flow regulation effectively reduced the population size of both simuliids and trichopterans during 1978 and of simuliids during 1980. This was particularly noticeable in 1980 when the large population of Simuliidae between June and July did not develop into the expected large population seen in October of the previous years. The increase of small hydropsychid and *C. thomasseti* larvae in October, which was not interrupted by water flow regulation that year, could effectively contain population growth of *S. chutteri* within acceptable levels (de Moor 1982a). During 1979 when the population size of simuliids increased between August and October the appearance of *C. thomasseti* larvae was undoubtedly the major factor causing their decline in November as no water flow regulation was implemented that year.

Fig. 9. Clustering of simuliid larvae and pupae observed on stones exposed after a drop in the water level following water flow regulation. These stones during flow conditions exceeding 3 m^3s^{-1} are in swift flowing regions (*c* 1 ms^{-1}) of rapids in the Vaal River.

Predation by *C. thomasseti* was more intense when the population size of simuliids was high. Predation by hydropsychids on simuliids occurred even when population levels of the latter were low and this would typify a density independent type of predation. When population levels of simuliids were high a larger percentage of developing hydropsychid larvae would find sufficient food and this would then lead to a larger population of predators (Fig. 7). The effectiveness of *C. thomasseti* larvae as predators was mainly due to the fact that the larval life cycle of this species coincided with high population levels of the aquatic stages of simuliids in spring. The larval drifting behaviour of *S. chutteri* which made it a successful coloniser of newly inundated regions (Chutter 1968, de Moor, Chutter and de Moor 1986) also made it susceptible to predation by net-spinning Hydropsychidae.

Other potential specialist predators would be the mochokid rock catlets belonging to the genus *Chiloglanis*. Their close co-existence with simuliid larvae and pupae in swift-running-water biotopes makes them preadapted to being specialised predators of Simuliidae.

For simuliid larvae, escape and avoidance mechanisms from predators work most efficiently in their natural swift-flowing-water biotope. The larvae usually avoid contact with a predator by attaching a silk life line, releasing hold of their substrate and drifting downstream in the current for a limited distance before resettling. Because of the swift current most other aquatic invertebrates find it difficult to maintain a good grip on the substrate while moving about in the running water. For this reason inching away by using the slow looping locomotion, spinning a patch of silk hooking the

anterior proleg onto this and releasing the posterior proleg and then attaching this to the spun patch before unhooking the anterior proleg once more, is also an effective avoidance technique. In a slower current this advantage is lost and predators become much more efficient in locomotion and procuring of larval simuliid prey. This may explain the dense clustering and almost exclusive occurrence of large numbers of larvae and pupae of *S. chutteri* on certain stones collected from rapids (Fig. 9). Such densely colonised stones are found only in the swiftest of water flows where most other species of invertebrates and vertebrates in the Vaal River would find it difficult to obtain a hold on the substrate let alone actively prey on blackfly larvae and pupae. When water flow temporarily decreased, during flow regulation applied to control simuliid densities, a host of opportunistic predators sueh as birds, fish, crabs and several adult Diptera species made use of these conditions. They all concentrated around regions where flow was reduced to a trickle and commenced vigorous feeding on the simuliids left stranded. When mass emergences of adult *S. chutteri* occurred in spring predation on adults was also noted to be intense.

Even though there was an abundance of larvae and pupae of *S. chutteri* in the Vaal River near Warrenton their specialised adaptation to exist in the swiftest of water flows provides them with effective predator avoidance mechanisms. Their rapid breeding also allows for exponential population growth during periods when inundation of a previously dry river bed occurs or when larval populations of *C. thomasseti* decrease because the majority of individuals are pupating or emerging as adults. Hydropsychid larvae coexisting with simuliid larvae in the same biotope are able to exploit them as prey with a minimum of effort. Hydropsychid larvae can thus be considered as stones-in-current biotope, specialist predators and are therefore also exapted (*sensu* Gould and Vrba 1982) simuliid specialist predators. The mochokid rock catlets of the genus *Chiloglanis* also fit into this class of predator because of their biotope and feeding preferences. *Clarias gariepinus* exploiting the abundance of simuliid adults on the water surface is considered to be a generalist predator. Its opportunistic behaviour in exploiting the dense concentrations of pupae on stones, possibly when flow rates are sufficiently reduced to allow them access to the normally swift flowing rapids where water velocities are in excess of 1 ms^{-1}, makes it an opportunistic generalist able to take advantage of conditions outside its normal feeding behaviour pattern. Most of the other predators discussed above are random generalist predators. They use their normal feeding behaviour approaches and switch to concentrated feeding on simuliids when these become abundantly available.

Some of the species such as *Salifa perspicax* which is a voracious predator on simuliid larvae were only rarely found coexisting with dense populations of Simuliidae. They could thus not be considered as biotope specialist predators even though they would apparently be able to successfully maintain their position on substrates in swift flowing waters.

If predators are to be used in conjunction with other methods to keep population growth of simuliids under control, a detailed ecological assessment of the life history of the predators to be used should be undertaken. It is important to identify factors that will optimize environmental and developmental conditions for the predator and hence increase the chances of efficient control of the target prey species.

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Three recently erected Trichoptera families from South Africa, the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae (Integripalpia: Sericostomatoidea)

by

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(Albany Museum, Grahamstown)

with

A cladistic analysis of character states in the twelve families here considered as belonging to the Sericostomatoidea

by

F.C. DE MOOR
(Albany Museum, Grahamstown)

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ABSTRACT

Three southern African families of Trichoptera, the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae, erected recently (Scott, 1985) to accommodate the genera *Hydrosalpinx*, *Petrothrincus* and *Barbarochthon* (all Barnard 1934), are fully described, illustrated and discussed. As far as is known all three genera are endemic to South Africa and appear to be relicts of the Gondwanan south temperate fauna. They are largely confined to the western, southwestern and southern coastal folded belt. *Petrothrincus* and *Barbarochthon* have also been recorded from the eastern Cape Province and *Barbarochthon* from Natal.

Specific descriptions are given for the single species of *Hydrosalpinx* and *Barbarochthon*, and for the three species, one new, of *Petrothrincus*. A key to the species of *Petrothrincus* is given.

The three families are placed in the superfamily Sericostomatoidea Stephens 1836, *sensu* Weaver 1983 of the suborder Integripalpia.

Phylogenetic relationships of the twelve families considered to belong to the Sericostomatoidea are investigated using cladistic methods.

INTRODUCTION

Several southern African genera of Trichoptera have presented difficulties in classification since their original description by Barnard (1934). These genera include *Rhoizema, Cheimacheramus, Petroplax* and *Barbarochthon,* all accommodated by him in the family Sericostomatidae Stephens 1836 (emend. McLachlan, 1874), in its old wide sense. Others are *Hydrosalpinx* and *Petrothrincus,* placed by Barnard under Aequipalpia near, but not in, the families Molannidae and Beraeidae. To Barnard's group Morse (1974) added a new genus *Aclosma* which he attributed to the Sericostomatidae *sensu stricto.* This genus he erected for his new species *A. bispinosa* from Natal. He believes that *Petroplax anomala* Barnard from the eastern Cape should also be included in his genus *Aclosma* (Morse *in litt.*, 15.xi.1974). The differences between *Aclosma* and *Petroplax* are small and *Aclosma* may prove to be a junior synonym. All the above genera appear to be endemic to South Africa and restricted mainly to the mountains of the coastal folded belt in the Cape Province. *Aclosma* and *Barbarochthon* have also been found in Natal.

Over the years most of the older genera have suffered various vicissitudes, taxonomically speaking. Barnard himself did not indicate to which of the then existing subfamilies he considered that *Rhoizema, Cheimacheramus, Petroplax* and *Barbarochthon* might belong. He did, however, comment that the family Sericostomatidae was a repository for a number of forms the systematic position of which was not clear. Shortly afterwards Lestage (1936), terming the Sericostomatidae *sensu lato* "this old curiosity shop" as had McLachlan earlier, suggested that *Rhoizema, Cheimacheramus* and *Petroplax* might belong to the Sericostomatinae but remarked that the whole family diagnosis needed revision with the creation of a special division for *Petrothrincus* and *Hydrosalpinx.* He considered that *Barbarochthon* was more likely to belong to the Brachycentrinae than to the Sericostomatinae on account of the structure of the maxillary palps. Ulmer (1955) followed Lestage in placing *Barbarochthon* under Brachycentrinae with a query but remarked that the immature stages did not fit well there. Fischer (1970) allocated it to the Brachycentridae without comment. Marlier (1962) reunited all four genera (*Rhoizema, Petroplax, Cheimacheramus* and *Barbarochthon*) in the Sericostomatinae as an expedient, though artificial, temporary measure pending revision when greater knowledge should become available.

After consultation with Dr G.B. Wiggins and comparison with Canadian material kindly sent by

him, it was decided that *Rhoizema, Cheimacheramus, Petroplax* and *Aclosma* could well be accommodated in the Sericostomatidae *sensu stricto* as at present understood, together with *Aselas* Barnard, another endemic genus, more classically sericostomatid than the other four. *Barbarochthon* does not, however, belong to this family.

Although, seen in life, adults of both *Petrothrincus* and *Hydrosalpinx* somewhat resemble sericostomatids in appearance and posture they do not fit into the Sericostomatidae, primarily because the males have five-segmented maxillary palps similar to those of the females. Barnard (1934) contented himself with placing both under Aequipalpia, commenting that they might be included in the Molannidae-Beraeidae were it not for the presence of a discoidal cell in the fore wings. He also commented (p. 323) that "the genus [*Petrothrincus*] bears a general resemblance to *Thremma* in the venation of the female, and the scutiform larval case. There are several peculiarities, however, in the venation, including the dissimilarity in the sexes. The larval resemblances are evidently due to similarity of habitat, and do not necessarily indicate relationship." In that Barnard appears to be perfectly correct. The two families show such major differences that *Petrothrincus* cannot possibly be accommodated in the Uenoidae: Thremmatinae (in which *Thremma* is now placed). Lestage (1936) discussed their position in some detail, but left it open, suggesting (as mentioned above) that they be placed in a special division, a division more primitive than the Molannidae in its retention of the discoidal cell in the fore wings, and heralding the Beraeidae in larval type. Ulmer (1955) placed *Petrothrincus* in the Helicopsychidae with a query. Fischer (1964) put it into the Molannidae, leaving *Hydrosalpinx* as *incertae sedis,* quoting Scott (1967) as tentatively placing it in the Beraeidae. Fischer was under a misapprehension since in Scott's preliminary key the family Beraeidae was keyed out *per se,* followed by a note that *Hydrosalpinx* and *Petrothrincus* did not entirely agree with that family as diagnosed and had therefore been given separate positions in the key under their generic names. Marlier (1962) left both genera as *incertae sedis,* pending a world revision. When the present author originally started to construct keys to southern African Trichoptera, it was found convenient at both adult and larval levels to lump the five sericostomatid genera together with *Barbarochthon* in a heterogeneous group as "western Cape sericostomatids". *Hydrosalpinx* and *Petrothrincus* were keyed out separately as genera. More recently, however, when revising the keys to Afrotropical families, the author had occasion to study all the southern African genera in detail and with more experience, and tried again to fit *Barbarochthon, Hydrosalpinx* and *Petrothrincus* into those families from elsewhere that appeared to be nearest to them, but again without success. It would only be possible to do so by altering the family diagnoses to fit, not a very desirable or satisfactory procedure, particularly for endemic genera from another part of the world.

After much consideration and subsequent consultation with Dr F. Schmid, Professor G.B. Wiggins and Dr A. Neboiss, the author decided to erect three new families, the Hydrosalpingidae, Barbarochthonidae and Petrothrincidae, to accommodate them. This brings southern Africa more into line with the Australian Region where several new families have been erected to accommodate endemic genera which did not fit into existing families although they had previously been allocated to one or another of the older families despite the difficulties encountered in so doing.

The original intention had been to erect the three new families in the present paper. As it transpired, however, they were unintentionally, but validly, erected in the chapter on Trichoptera (Scott, 1985) for the book *Insects of Southern Africa* (Scholtz and Holm, 1985). This poses problems to research workers because the families were not formally erected nor do they appear under the author's name. The present paper, although long delayed by the author's illness, fills the lacunae, providing the necessary descriptions, illustrations and discussion. In addition cladistic analyses of the phylogenetic relationships of the twelve families considered to belong to the Sericostomatoidea are presented by

Dr F. C. de Moor.

A diagnosis is given for each of the proposed new families, all of which are monogeneric. In view of the fact that two of the three genera on which the families are based are also monotypic, namely *Hydrosalpinx* and *Barbarochthon*, it has been decided in those cases to omit a generic diagnosis as it is covered by the full description of the species. As Wiggins (1984) has pointed out, the diagnostic characters of a monotypic genus are not objectively separable from those of the species. In the third genus, *Petrothrincus*, there are three species, two known and one described in this paper, making a separate diagnosis for the genus possible. Comments on such biological aspects as are known for each genus are given.

Fully illustrated descriptions of the type-species of each of the three genera and therefore of the three families are given. These include descriptions of the male and female imagos, and the larva and pupa together with their cases. With respect to *Petrothrincus* differences between the type-species, the second known species and the new species are noted, the two latter are described briefly and illustrated, and a key to the species is provided. The possible origins of the three families are discussed.

In this paper southern Africa is regarded as being delimited to the North by the Cunene, Okavango and Zambezi rivers, including their watersheds but excluding Lake Malawi. The north-flowing rivers on the other side of the watershed are regarded as central African.

Geographical references are taken from 1:50 000 maps, each of which covers a quarter degree square. Each degree square is numbered and divided into 16 such maps (15' x 15' squares). As an example 3318 AB refers to a map between 33° to 33°15' S and 18° 15' to 18°30' E (see Leistner and Morris 1976, introductory 4 pp.). Indication of localities in this way is necessary as older localities are often not precise and may refer to a range of mountains or a whole river.

Abbreviations and names of collectors cited in the text are as follows: ACH - A.C. Harrison; ADH - A.D. Harrison; BCW - B.C. Wilmot; DFH - D.F. Houck; FCdM - F.C. de Moor; FMC - F.M. Chutter; HB - H. Bertrand; HGW - H.G. Wood; HM - H. Malicky; HMB - H.M. Barber; JDA - J.D. Agnew; JMK - J.M. King; KHB - K.H. Barnard; KMFS - K.M.F. Scott; NK - N. Köhly; RD - R. Dick.

THE THREE RECENTLY ERECTED FAMILIES

Family Hydrosalpingidae Scott 1985

Hydrosalpingidae Scott 1985: 331, 337; Scott 1986: 231, 234 (table 1).

Type-genus *Hydrosalpinx* Barnard 1934: 321, 323.

The family Hydrosalpingidae was erected to receive the single genus *Hydrosalpinx* Barnard. One species of *Hydrosalpinx*, *H. sericea* Barnard, is known. It has been recorded from a number of mountain streams in the western and southwestern Cape Province.

Recognition

Imago medium-sized, hairy, golden-brown. Maxillary palps 5- segmented in male and female, very long in male. Labial palps 3- segmented, very long in male. Pronotum with 1 pair warts; mesonotum without warts, usually with a pair of single setae; scutellum with single large wart with lateral setae.

Family diagnosis

Male imago

Ocelli absent; eyes large, glabrous; vertex with pair of small inter-antennary setose warts and pair of large, subtriangular posterior setose warts, also with pair of small tubercles, one on each side of median sulcus. Antennae slightly longer than fore wings; scape stout, slightly shorter than head; flagellum tapered. Maxillary palps very long, 5-segmented, with fifth segment longest, not annulate. Labial palps long, 3-segmented, with third segment longest, not annulate.

Pronotum with single pair of large warts; mesonotum without warts; scutellum elongate with single large sub-oval wart bearing lateral setae. Tibial spurs 2, 2, 4; some tibial and tarsal segments with double row of small black spine-like setae and several similar setae at most tarsal apices. Fore wings with discoidal cell closed, thyridial cell very long, forks 1, 2, 3 present, fork 5 absent. Hind wings with discoidal cell open, R_2 and R_3 fused; fork 2 only present. Wing-coupling macrotrichia present along part of costal margin of hind wings, linking with inturned anal margin of fore wings.

Genitalia with branched paired claspers (inferior appendages) arising from ninth segment; paired preanal appendages arising from tenth segment which is long; aedeagus large, simple; parameres absent.

Female imago

Larger than male and with more complete wing venation, the discoidal cell being closed in both fore and hind wings, although in the latter the closure may be unclear. In the fore wings forks 1, 2, 3 and 5 are present, as Cu_1 is forked. In the hind wings R_2 and R_3 are separate, so forks 1 and 2 are present; R_2 is complete. Other characters as in male.

Genitalia with simple dorsal plate (presumably those of ninth and tenth segments fused). Sternites of tenth segment unsclerotized; pair of terminal appendages visible, very small.

Larva

Case-dweller; larva not flattened; head, pro- and mesonota strongly sclerotized; no prosternal horn. Head rounded; frontoclypeal apotome with one pair of indentations; antennae very small, at base of mandibles; eyes prominent, set fairly far forward; mouthparts small; ventral apotome a short triangle, not completely separating the genae, only clearly seen in juveniles. Metanotum membranous with single pair of small sclerites. Fore legs stout, middle and hind legs slender. First abdominal segment with flattened dorsal hump, lateral humps each with a small, oval, dorsally pubescent sclerite; abdominal segments smooth, lacking setae; lateral fringe absent; lateral tubercles present on eighth segment; gills absent; ninth segment with a dorsal sclerite. Anal prolegs very short, their bases fused to form an apparent tenth segment; anal claw with one or two dorsal hooks.

Larval case

A somewhat tapered, gold-coloured, silken tube with slightly flared opening and terminal membrane pierced by a circular aperture.

Male pupa

No male pupae were available to the present author, however, according to Barnard (1934) the male is similar to the female but smaller and has very long maxillary and labial palps as in the imago.

Female pupa

Antennae slightly longer than body; labrum semicircular with short median lobe; mandibles strong with pointed apex, inner margin strongly serrated; maxillary palps only reaching end of metanotum; labial palp shorter. Middle tarsi fringed for swimming. Lateral abdominal fringes present, conspicuous, with tufted ends; gills absent; wing sheaths reach beginning of seventh abdominal segment. First abdominal segment without lappets; second to sixth segments with pre-segmental dorsal plates; fifth segment with postsegmental dorsal plate; all dorsal plates small. Anal appendages slender, rod- like.

Pupal case

An altered larval case, closed anteriorly and just behind the pupa with new membranes, each with a slit, with old posterior membrane persisting, and attached anteriorly with a single dorsal holdfast.

Genus *Hydrosalpinx* Barnard 1934

Hydrosalpinx Barnard 1934: 321, 323, Figs 16a-o.

Type-species *H. sericea* Barnard 1934.

Etymology: Generic name feminine, meaning a water trumpet; specific name, referring to silk; both names being descriptive of the case.

As *Hydrosalpinx* is a monotypic genus a generic diagnosis is omitted. It is covered by the full description of the species.

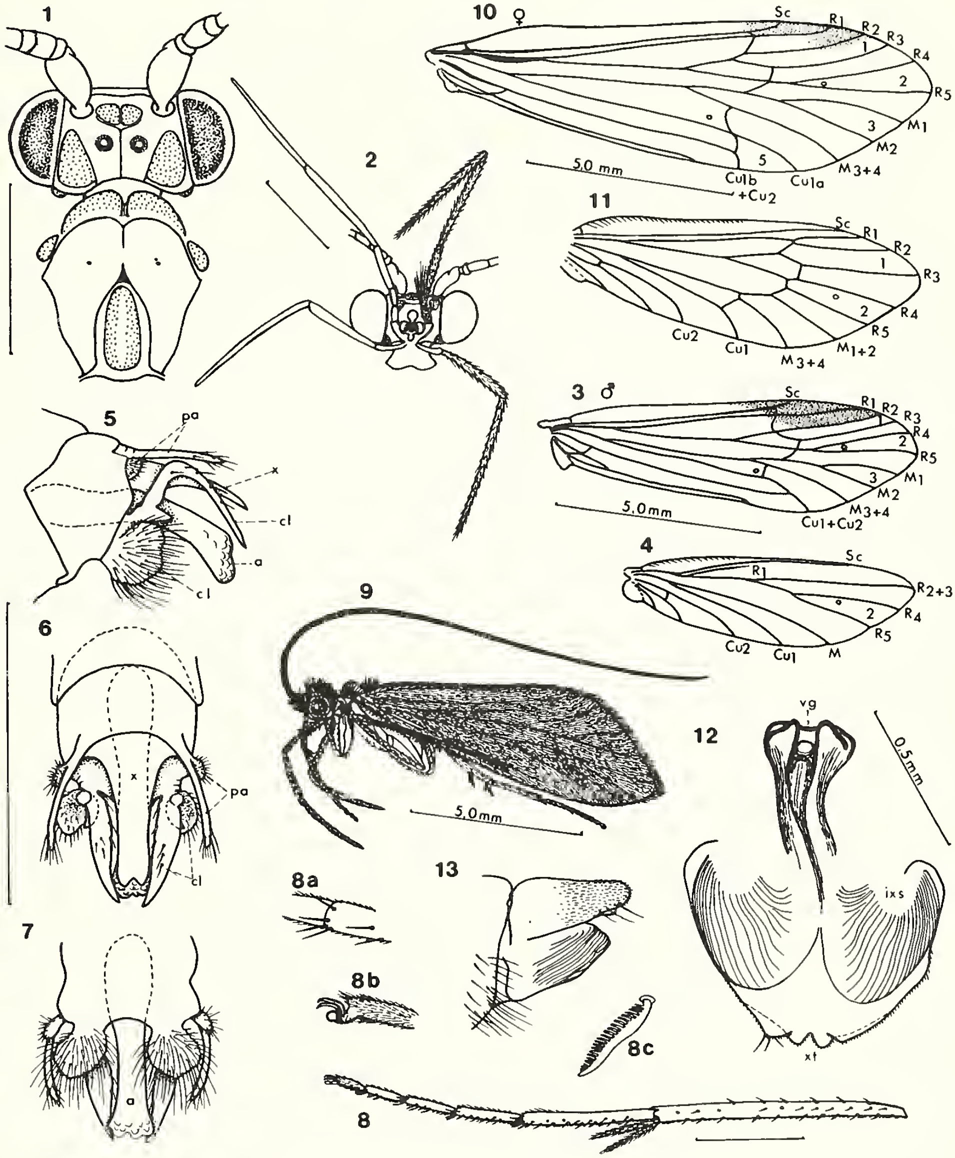
***Hydrosalpinx sericea* Barnard**
(Figs 1-32)

Hydrosalpinx sericea Barnard 1934: 321, 323, figs 16a-o (male, female, larval and pupal parts, pupal case); Scott 1985: 337, figs p (p. 331), v (p. 332); Scott 1986: 232, 236, 243.

Lectotype male here selected and designated from Barnard's syntypes, South African Museum, Cape Town.

Type locality: western Cape Province, Bain's Kloof, Wellington Mts, [3319 CA].

Barnard did not as a rule select types, the specimens in his collection being unmarked apart from name, locality, collector(s) and date. A Lectotype has been selected from those specimens listed in



Figs. 1-13. HYDROSALPINGIDAE : *Hydrosalpinx sericea* Barnard, male, female (Scale lines = 1 mm unless otherwise indicated). Material used: KHB

1. male: Head, pro- and mesonota, dorsal. 2. male: face, showing maxillary and labial palps. 3, 4. male: fore and hind wings. 5, 6, 7. male genitalia, lateral, dorsal and ventral views (a - aedeagus, cl - clasper, ic/icl - internal branch of clasper, pa - preanal appendage, x - hood formed by tenth tergum) . 8. male: left middle leg, tibia and tarsus, 8a, tarsal apex with crown of spinelike setae, 8b, fifth tarsal segment with claw, 8c, single plumose spinelike seta, all further enlarged. 9. male: entire insect, lateral. 10, 11. female: fore and hind wings. 12, 13. female: genitalia, ventral and lateral views (ixs - ninth sternite, ixt - ninth tergum, vg - vagina, xt - tenth tergum) (13 after Barnard 1934 fig. 16h).

his 1934 paper and still remaining in the South African Museum collection. It is the best available male (not perfect but nearly so, right fore leg and labial palp only being missing) and is from Bain's Kloof (14.iv.1933). The other specimens are regarded as Paralectotypes. The extant material and original records are listed after the descriptions of the different stages.

DESCRIPTION OF IMAGOS (Figs 1-13).

Male imago (Figs 1-9)

Medium-sized, hairy; fore wings 9-10 mm in length.

Colour description given by Barnard, probably from freshly pinned specimens - "Head and thorax fulvous with, pale golden hairs. Legs and antennae ochraceous or fulvous, the latter darker proximally. Wings thickly pubescent; fore-wings bright golden-brown, the costal area and the apical cells duller and darker brown, the veins paler and brighter; hind-wings greyish-brown, fringe grey."

Further description from male imagos, pinned and in spirit, from Barnard's collection.

Ocelli absent; eyes large, black, glabrous; vertex with a pair of small inter-antennary warts, a pair of large postero-lateral warts and a pair of bare median protuberances (Barnard's conical warts); mid-cranial sulcus complete (Fig. 1). All warts on head and thorax bear long, upstanding golden setae. Antennae longer than fore wings; scape stout, slightly shorter than head, with long setae; flagellum basally thick (less so than scape), tapering to slender tip. Maxillary palps (Fig. 2) laterally flattened, 5-segmented, very long (5.0 mm), with first and second segments very short, third about equal to first and second together, fourth more than double length of third, fifth a little longer, simple, with second segment bearing several long dorsal setae. Labial palps 3-segmented, long, with first segment short, second longer, third longest, simple (length 4.0 mm).

Pronotum with single pair of large warts; mesonotum without warts; scutellum elongate, subtriangular, with single large suboval wart bearing scattered setae. Legs with tibial spurs 2, 2, 4: fore and middle tibiae and tarsi and hind tarsi with double or treble row of black spinelike setae, and with a crown of three or four similar setae at tarsal apices on middle and hind legs (Figs 8 and 8a, b). These spinelike setae are plumose (Fig. 8c). Wings (Figs 3, 4, 10, 11) with venation differing in both wings in the two sexes. Male fore wings (Fig. 3) with discoidal cell closed, median cell open, thyridial cell very long; there are forks 1, 2, 3 and a large jugal lobe; M is 3-branched; Cu_2 joins Cu_1, $A_1 + A_2$ join basally, meeting the hind margin at the arculus. Male hind wings (Fig. 4) with discoidal cell open; only basal part of R_1 present, R_2 and R_3 fused, M and Cu_1 unbranched, fork 2 only present and jugal lobe rounded and inturned. Corneous points present in both wings in fork 2 and in the thyridial cell in the fore wings. (Barnard gave the male fore wings forks as 1, 2, 3, (5), remarking that fork 5 was spurious owing to Cu_1 not being forked; it appears preferable to omit it, as the area between Cu_1 and M_{3+4} cannot be mistaken for a true fork 5.) The hind wings bear long macrotrichia (not hamuli) on the basal part of the costa, evidently linking with the inturned hind margin of the fore wings in flight. There is a long setal fringe along the anal margin of the hind wings.

The dorsum of the abdomen bears a pair of oval setose warts on each segment except the first.

Genitalia (Figs 5-7) with ninth and tenth tergites dorsally fused; paired preanal appendages arising from tenth segment near junction with ninth, long, slender, with blunt apices bearing a few setae, and small setose basal lobe. Tenth tergite forms a median dorsal apical hood with bifurcate apex, transparent and difficult to see. Claspers with lower branch broadly lobate, rounded and setose in lateral view, with upper branch sinuously blade-shaped, strongly curved dorsally, posteriorly and inwards with a stout triangular process near base and with a few setae. In the two pinned specimens

the upper branches cross over one another dorsally. Aedeagus stout, lacking parameres or endothecal processes.

Female imago (Figs 10-13)

Larger than the male (fore wings 11-12 mm). Palps similar but shorter (maxillary palps 3.0 mm, labial palps 1.5 mm in length); otherwise very similar apart from wing venation and genitalia, which are dealt with below.

Wing venation more complete than in male, the discoidal cell being closed in both fore and hind wings, although in the latter the closure may be unclear. In the fore wings forks 1, 2, 3 and 5 are present as Cu_1 is forked. In the hind wings R_2 and R_3 are separate, so forks 1 and 2 are present; R_1 is complete.

Genitalia (Figs 12, 13) with ninth and tenth tergites apparently fused, simple, rounded, partly pubescent, with a few longer lateral setae, apex slightly projecting, bilobed, without appendages; sternal plates of ninth segment unsclerotized or only slightly so, rounded, with numerous striae or corrugations, vagina strongly sclerotized; sternum of eighth segment thickly setose along posterior margin.

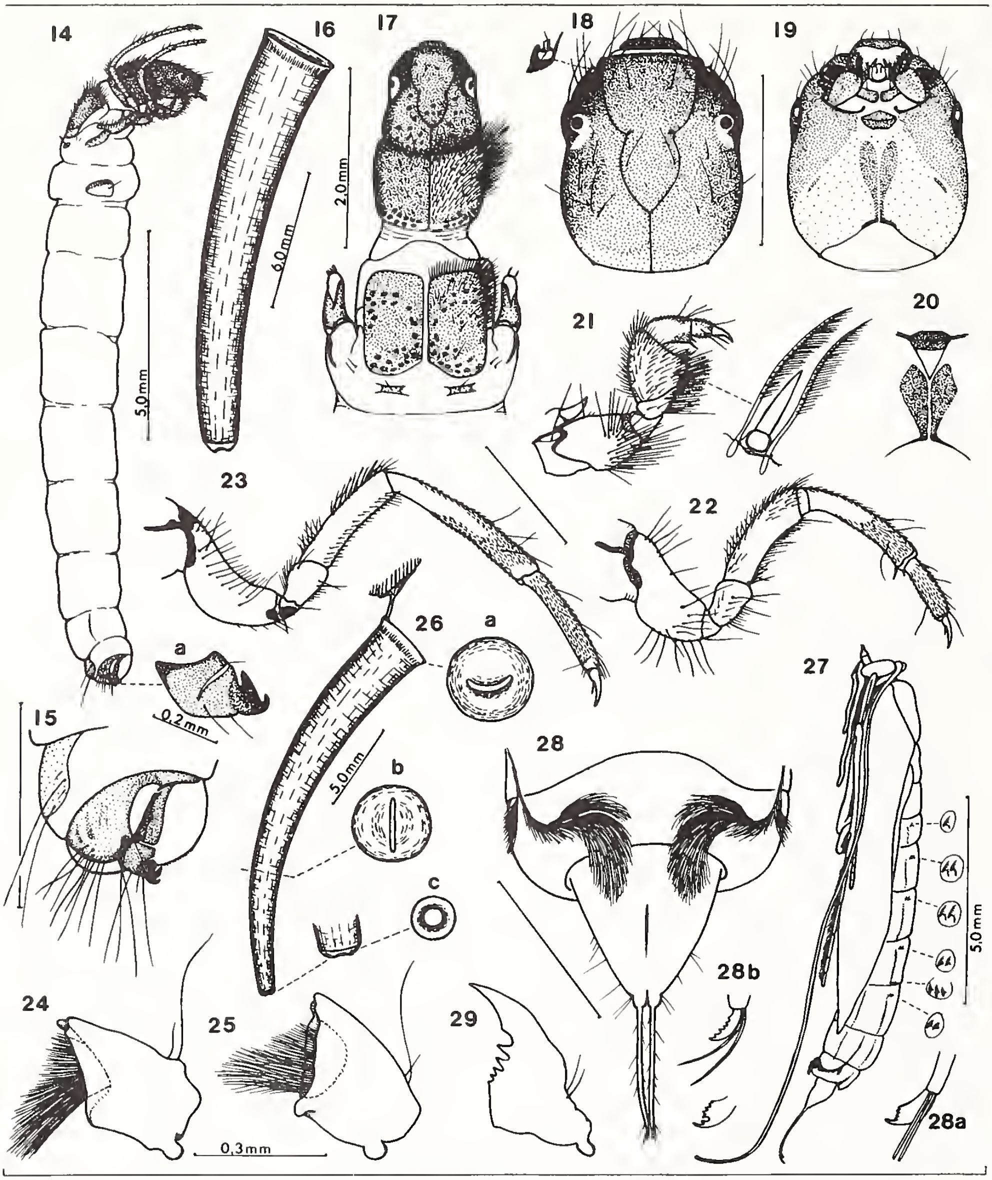
DESCRIPTION OF MATURE LARVA (Figs 14-25, 30-32).

The following description was made from material (MISC 306a) (in spirit) collected in 1976 from a mountain stream, tributary of the Vet River, Garcia's Pass, north of Riversdale in the southwestern Cape, which was compared with the earlier specimens from the western Cape and Barnard's own material, descriptions and drawings.

Case dweller; length 15-16 mm; larva not flattened.

Head (Figs 17-20, 31, 32) slightly longer than broad, very dark brown; cuticle strongly sclerotized, pitted; muscle spots smooth, shining, colour as head; genae paler; frontoclypeal apotome with single pair of lateral indentations; ventral apotome short, triangular, darker brown anteriorly, pale posteriorly, triangular shape only discernible in young larvae (Fig. 20); ventral ecdysial line unclear or absent; pair of brown pigmented areas present lateral to mid-line. Eyes prominent, situated fairly far forward, beneath a short, strong ridge, giving a faintly `beetle-browed' effect, each eye in a clear area under cuticular lenses. Antennae inconspicuous, at bases of mandibles. Labrum small with rounded anterior margin, partially retractile. Labium with clear paired labial palps. Maxillary palps stout, 5-segmented, strongly setose; galeae also long, stout; stipites large. Mandibles (Figs 24 and 25) small, heavily sclerotized, hollowed on inner side with strong brushes, two small apical teeth and two setae on outer side of each.

Thorax (Figs 14, 17) with prosternal horn absent. Pronotum without carina or anterolateral expansions, mainly very dark brown and thickly set with long, fine setae, posterior part paler with dark spots and few setae. Pleural sclerites (Fig. 21) light brown; pre-episternum strong, curved, pointed, not fused with episternum. Mesonotum with large oblong paired plates, dark brown anteriorly, paler posteriorly, with dark spots; plates with many relatively long, fine, pale, inconspicuous setae, mainly anterolaterally. Metanotum membranous apart from a pair of very small, transversely oblong, lightly sclerotized plates, each with a single seta. Sternum membranous. Fore leg (Fig. 21) shortest, stout; coxa with long, mainly ventrally placed setae; trochanter divided, proximal part bare, distal part with ventral trochanteral brush; femur widely subtriangular, with many fine setae and long ventral



Figs. 14-29. HYDROSALPINGIDAE: *Hydrosalpinx sericea* Barnard, mature larva, pupa and cases
(Scale lines = 1 mm unless otherwise indicated).
Material used: larva MISC 306a; pupa KHB
14. Mature larva, habitus, lateral, a, anal claw, much enlarged. 15. Anal region, further enlarged. 16. Larval case. 17. Head and thoracic nota, dorsal view (setae shown only on right thoracic nota), muscle spots indicated. 18. Head, dorsal with antenna fur ther enlarged. 19. Head, ventral. 20. Ventral apotome of young larva. 21. Right foreleg, with plumose and bladelike setae further enlarged. 22, 23. Right middle and hind legs. 24. Right mandible, dorsal view. 25. Left mandible, ventral view. 26. Pupal case showing holdfast; a,b,c, membranes closing front aperture, end of part of case occupied by pupa and hind aperture respectively (after Barnard 1934 fig. 160). 27. Immature pupa, female, habitus, with dorsal plates further enlarged showing hooks. 28. Apex of abdomen; apices of anal rods (appendages) shown further enlarged, a. of specimen drawn, b. variations (after Barnard 1934 fig. 16m). 29. Left pupal mandible.

fringe, like that of trochanter including feathered setae and strong blade-like bristles; tibia with small distal ventral protuberance bearing two spinelike setae; tarsus smaller; claw stout, sharp, about same length as tarsus, with long basal seta. Middle leg (Fig. 22) longer, hind leg (Fig. 23) longest, similar in form, each with long, curved coxa, short divided trochanter (proximal part small, distal part apically widened, rounded); femur shorter than tibia, noticeably so in hind leg; tarsi and parts of tibiae finely pubescent in both; tarsal claw considerably shorter than tarsus with small basal seta part way along claw.

Abdomen (Figs 14, 15, 30) smooth, creamy white, with segmental divisions shallow, setae lacking or minute, no lateral fringe visible (feeble according to Barnard), gills absent; first segment with flattened dorsal protruberance and lateral protuberances, lateral humps each with an oval faintly sclerotized area bearing an anterior pubescent patch and a single seta; eighth segment with row of about 24 lateral tubercles on each side; ninth segment with very pale dorsal sclerite bearing two pairs of long posterolateral setae; apparent tenth segment (fused bases of paired anal prolegs) short, rounded, not produced into apical lobes or projections, with few setae; anal prolegs with large curved lateral sclerites almost meeting ventrally, bearing long apical setae, sclerotization variable with darker and paler areas. Ventral sole plates with dark dorsal margin; anal claws small, strong, with one or two stout, curved accessory hooks.

Larval case (Figs 16, 30)

Composed entirely of brighter or darker gold-coloured silk, tubular, widening anteriorly to the slightly flared aperture; posterior aperture circular, centrally placed on raised membranous base. Young larvae have a few sand grains incorporated near base of case; very early instars have a small sand-encrusted basal section; this section is evidently cut off later. Length of case (mature larvae) 17-18 mm.

Note on identification of larvae and cases of *Hydrosalpinx*: the golden, silken larval case is distinctive and easily recognizable. Care, however, must be taken to identify the larva itself, as empty cases are frequently utilized by larvae of *Athripsodes* species (Leptoceridae) which are usually found further down stream below the habitat of *Hydrosalpinx*. The antennae of the *Hydrosalpinx* larva are very small (Fig. 18) whereas those of *Athripsodes* are very long. Furthermore, the *Athripsodes* larva usually adds a collar of sand grains to the case.

DESCRIPTION OF PUPA (Figs 26-29).

The description of the pupa is based on the single available specimen, a damaged immature female, and on Barnard's description and drawings.

Male and female pupae

Antennae longer than body. Labrum semicircular with short median lobe. Maxillary and labial palps very long in male, somewhat shorter in female. Mandibles stout with broad base, strongly dentate inner margin and two dorsal setae (Fig. 29). Middle tarsi fringed for swimming. Lateral fringes present on seventh abdominal segment, curving round onto eighth, forming strong ventral tufts as indicated (Figs 27, 28). Gills absent. Presegmental dorsal plates on second to sixth abdominal segments (one hook per plate on second, two on third to sixth); postsegmental plates on fifth segment (three anteriorly directed hooks per plate). Anal appendages rod-like, slender, with scattered setae; dorsally

curved apices serrated with apical finger and two stout setae (Figs 28a, b).

Pupal case (Fig. 26)

An altered larval case, fastened to a rock or stone by a single anterodorsal attachment disc. Hind end closed by the larval membrane with a circular aperture. Posterior part of the case closed off from the section in which the pupa lies by a new membrane with a narrow vertical opening. Anterior end of case closed by a membrane with a transverse crescent-shaped slit on a central boss (Fig. 26c, b, a).

DISTRIBUTION

South Africa, mountain streams in the coastal ranges in the western and southwestern Cape Province.

MATERIAL EXAMINED

South African Museum material

Material in spirit

Lectotype: western Cape: Bain's Kloof, east side [3319 CA] (KHB, 14.iv.1933, male).

Paralectotypes: Western Cape: Bain's Kloof, east side [3319 CA] (KHB, 14.iv.1933, 5 males, one with head off and genitalia of two in microvials, 1 female abdomen lacking genitalia).

Other material: western Cape: Bain's Kloof, east side [3319 CA] (KHB, 14.iv.1933, an immature pupa); Bain's Kloof (larvae); Du Toit's Kloof [3319 CB] (CWT and HGW *leg*., 1.iv.1934, KHB det., 6 males, one lacking abdomen).

All the specimens are faded and most are more or less damaged.

Pinned material

Paralectotypes: Western Cape: Bain's Kloof (KHB, 1.v.1933, 2 males); Hottentots Holland Mts [3418 BB] (3000 ft. [= 914 m] KHB, March 1919, 1 female).

The males with wings spread are entire but the palps are much distorted, some curled up and some broken. The female, the only one still available, had had the wings spread but one pair and the abdomen had been removed and tipped onto card points by Barnard. The present author removed the fore wing (which was damaged) and the abdomen from the card points. She mounted the fore wing on a celluloid strip, removed, cleared and mounted the genitalia in Euparal on another celluloid strip and placed both on the pin with the specimen. The hind wing was found to be almost entirely missing.

Albany Museum material

Material in spirit

Western Cape: Great Berg River, Fransch Hoek [Franschhoek] Forest Reserve, Assegaibos stream tributary [3319 CC] (GBG 2k: ADH, 24.v.1950, larva), Assegaibos cold stream waterfall

(GBG 132c: ADH, 20.xi.1950, larva and GBG 752a: ADH, 26.xi.1953, larvae), source of Berg River at Sneeugat 3319 CC (GBG 372a: ADH, 28.ix.1951, larva); stream on Helderberg Mt., near Somerset West, [3418 BB] (MISC 157c: DFH, iv.1963, 4 larvae).

Southern Cape: Vet River, Garcia's Pass, north of Riversdale, tributary below Tolhuis [3421 AA] (MISC 306a: KMFS, 9.ii.1976, 23 larvae).

MATERIAL CITED IN LITERATURE

Barnard (1934: 323): Hottentots Holland Mts [3418 BB] (KHB, 12 March 1919, 1 male, 1 female); Wolwenhoek Kloof, French Hoek [Franschhoek] [3319 CC] (KHB, April 1931, 1 male); Jonkershoek, Stellenbosch [3318 DD] (HGW, February and April 1931, male and female pupae); Bosch Kloof Keeromberg, Worcester [3319 DA] (KHB, January 1930, larvae); River Zonder End [Riviersonderend] Mts [3419 BA] (HGW, December 1931, larva); Cedar Mts [Cedarbergen], Clanwilliam [3219 AA] (KHB, January 1930, larvae); Du Toit's Kloof, Rawsonville [3319 CB] (KHB, March 1932, cases); Gt. Winterhoek Mts, Tulbagh [3319 CB] (KHB and HGW, November 1932, larvae); Bain's Kloof, Wellington Mts, [3319 CA] (KHB, 14th April 1933, males; KHB and HGW, 1st May 1933, males, females). All were deposited in the South African Museum, Cape Town. The extant material is listed above under material examined.

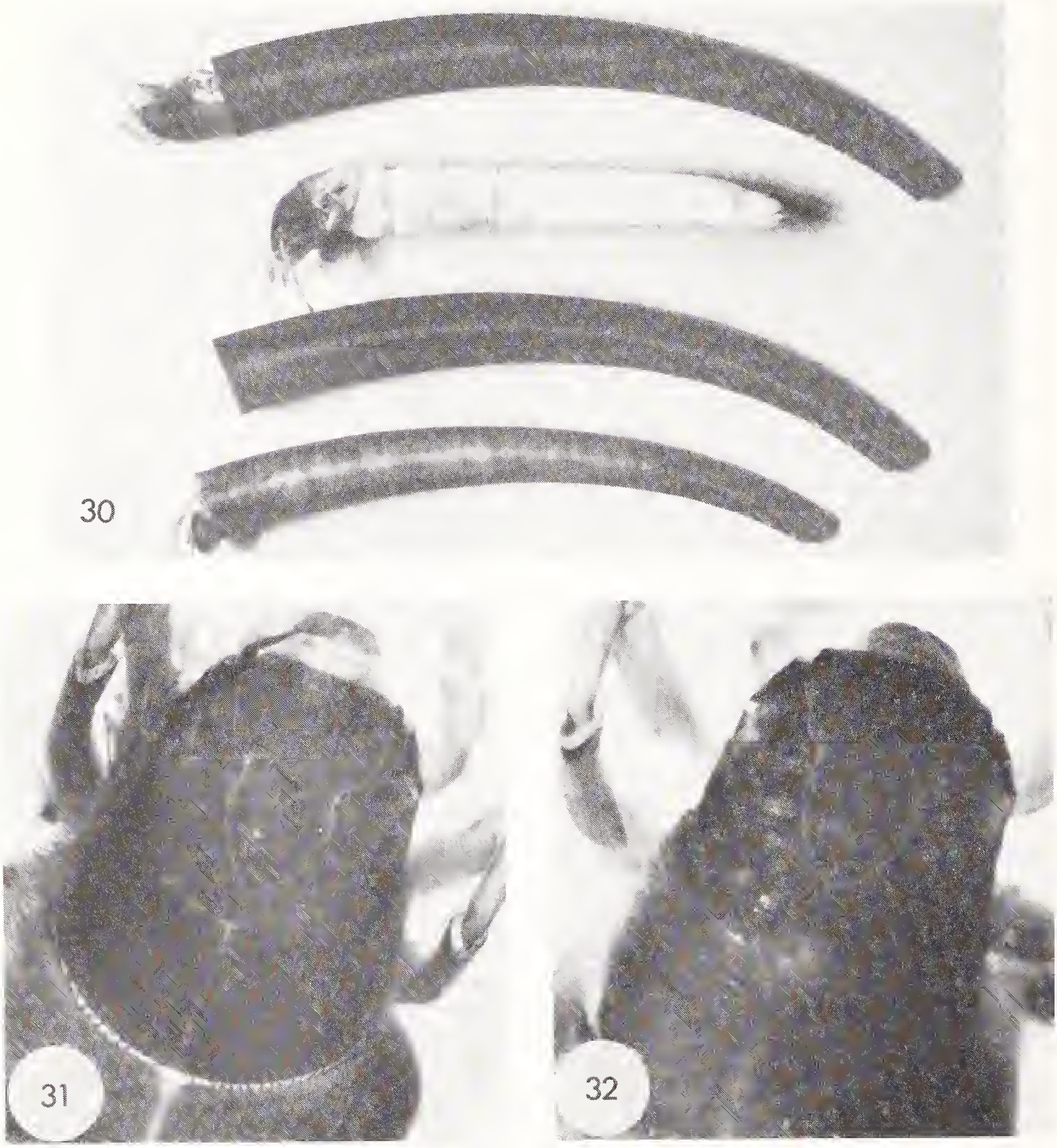
Jacquemart (1963: 347): Kogelbaai 10 miles south of the Strand, [western Cape] [3418 BD], shaded stream rushing down mountain slope, at road forming a waterfall, 19.xii.1950, larvae. The identity of these larvae is given by Jacquemart in his text as *Hydrosalpinx (sericea)*? and in the caption to his figure as *Hydrosalpinx sericea*. From a consideration of Jacquemart's drawings the present author concludes that they could be *Hydrosalpinx*, probably *sericea*. Unfortunately the cases were neither drawn nor described.

BIOLOGY of the genus *Hydrosalpinx*

Hydrosalpinx sericea larvae inhabit high-lying, cold, acid montane streams in which they are found in waterfalls, stony runs and riffles. Common in Barnard's day, this species is now rarely found, though it may still be locally common in remote areas. Its disappearance from some of the recorded localities is more likely to be due to alteration of river beds by the building of reservoirs and constant bush fires than to pollution, as this does not occur in them. As Barnard was a great mountain climber many of his collecting places are inaccessible to collectors who are not mountaineers.

The adults, at rest and in flight, can easily be confused with sericostomatids such as *Rhoizema* spp. being little smaller than the smaller species of *Rhoizema* and having somewhat similar colouring. They have been collected in March, April and May.

The larvae may be seen grazing on the stones or rocks of the substratum. The gut contents and mouthparts, particularly the mandibles with their small, blunt apical teeth and stout inner brushes, indicate that the food comprises algae and detritus together with any animalcules and bacteria present.



Figs. 30-32. HYDROSALPINGIDAE: *Hydrosalpinx sericea* Barnard, mature larvae.

30. Photograph of 2 mature larvae in cases and one ex case. 31, 32. Photographs of head of mature larva further enlarged. Photographs by J.C. Hodges, Jr. (Ex. MISC 306a).

Family Petrothrincidae Scott 1985

Petrothrincidae Scott 1985: 331, 337-338; Scott 1986: 231, 234 (table 1).

Type-genus *Petrothrincus* Barnard 1934: 323, 325.

The family Petrothrincidae was erected to receive the single genus *Petrothrincus* Barnard. Three species of *Petrothrincus* are known. Two occur in high mountain streams in the western Cape Province, having been collected together by Barnard at 4 000ft [= 1 219 m] in the Hottentots Holland Mountains. The distribution of *circularis* Barnard, however, extends further downstream than that of *triangularis* Barnard. The third species was found in similar streams in the southern Cape Province. It has been described in this paper as *P. demoori.*

Recognition

Imago small, dusky; fore wings may have light patches or appear plain grey. Maxillary palps 5-segmented in male and female. Pronotum with two pairs of warts; mesonotum with median patch of setae; scutellum with pair of anterolateral warts.

Family diagnosis

Male imago

Ocelli absent; eyes large, glabrous; vertex with pair of small interantennary setose warts and pair of large posterior warts, without tubercles. Antennae stout, somewhat longer than fore wings; scape about as long as head; flagellum tapered. Maxillary palps 5- segmented, fifth not annulate. Labial palps 3-segmented, third simple, not annulate. Palps of normal length.

Pronotum with two pairs of warts; mesonotum without warts but with median field of recumbent setae; scutellum quadrangular with pair of anterolateral warts. Tibial spurs 2, 2, 4. No black spinelike setae on legs but colourless spinelike setae are present. Fore wings with discoidal cell closed, thyridial cell long, Cu_1 simple; forks 1, 2, 3 present, Cu_2 complete. Hind wings with costal area proximally broad, Sc and R_1 close together, sinuous, base of R_{2+3} and discoidal cell absent, forming median discal area; M simple, joining Cu_1 about midway; only base of Cu_2 present. Wing coupling macrotrichia present on basal part of costa in hind wings.

Genitalia with ninth tergite narrow, fused to tenth, which is somewhat produced; preanal appendages prominent; paired spatulate claspers with internal branches arising from ninth; aedeagus accompanied by paired parameres; ninth sternite produced.

Female imago

Similar to male but slightly larger than male; antennae somewhat shorter. Fore wings similar to those of male, except for slight differences in base of anal veins. Hind wings also similar to those of male in regard to curvature of Sc and R_1 and broad basal costal area, however, base of R_{2+3} is almost entirely absent; M is 2-branched; M and Cu_1 join basally; Cu_2 is complete, as are 1A and 2A.

Genitalia with tenth tergite with apical projection, partly covered by a lightly sclerotized dorsal hood; a bilobed supragenital plate and simple or paired vulvar scales flanked by lateral striations, probably

modified pleural folds but at least partly sclerotized; appendages absent. Vagina small, sclerotized.

Larva

Case dweller; dorsoventrally flattened, widest at metanotum; head, pro- and mesonotum lightly sclerotized; prosternal horn absent. Head round, frontoclypeal apotome with one pair of indentations; antennae small, at base of mandibles; eyes small, fairly far forward; mouthparts stout, prominent; ventral apotome sub-oval, completely separating genae. Metanotum membranous (or with very weak median plate). Legs fairly long, with sparse long setae. Abdomen smooth, deeply indented ventrally; first segment with very large dorsal hump, lateral humps lacking sclerotized areas or setae; lateral fringe and lateral tubercles absent; gills present, small, branched or simple, varying according to species. Anal prolegs longer than usual in eruciform larvae, not fused basally; anal claws small with comb of small teeth.

Larval case

Larval case of fine sand grains, more or less limpet-shaped, circular to suboval or triangular, with ventral plastron supporting larva, and with posterodorsal terminal aperture.

Male pupa

Antennae much longer than body; labrum semi-circular; mandibles strong, triangular, with apex blunt and inner margin feebly serrated; maxillary palps 5-jointed, palps reaching end of metathorax. Fore and middle tarsi fringed for swimming; lateral abdominal fringes and gills absent; wing sheaths reach end of seventh abdominal segment. First abdominal segment with small pair of posterolateral lappets; third to sixth segments with presegmental dorsal plates; fifth segment with post segmental dorsal plate; all dorsal plates small and weak. Anal appendages slender, the apical portion set with blade-like bristles. No special pocket for male genitalia.

Female pupa

Similar to male but slightly larger; antennae much shorter than body, curled round at seventh or eigth segment meeting ventrally.

Pupal case

An altered larval case, with a transparent ventral membrane sealing off the anterior end from the plastron forwards, and sealed down around the edges onto the substratum (rock or stone).

Genus *Petrothrincus* Barnard 1934

Petrothrincus Barnard 1934: 323, 325-327, figs 17a-m, 18a-q.

Type-species *P. circularis* Barnard 1934, selected by Barnard, 1934.

Etymology: Generic name masculine, meaning coping-stones on a wall.

Generic diagnosis

Male imago

Small in size, densely hairy, with long fringe on posterior margin of hind wings.

Ocelli absent; eyes large, glabrous; vertex with pair of small inter-antennary warts and pair of larger rounded posterolateral warts; mid-cranial sulcus complete. Antennae stout, considerably longer than fore wings; scape stout, nearly length of head; flagellum tapered. Maxillary palps of medium length, 5-segmented, strongly pubescent, carried upwards over face. Labial palps 3- segmented, pubescent. In neither maxillary nor labial palps is the last segment annulate.

Pronotum with two pairs of warts, median pair long, outer pair very small; mesonotum without warts but with median area bearing short recumbent setae; scutellum quadrangular with large well defined pair of anterolateral warts. Legs with tibial spurs 2, 2, 4; middle and hind tibiae with a few colourless spine-like setae. Fore wings with discoidal cell closed, median cell open, thyridial cell long; Sc and R_1 running parallel, meeting costa separately; forks 1, 2, 3 present; Cu_1 and Cu_2 meeting margin separately; 1A and 2A joining before meeting margin; jugal lobe, small inturned. Hind wings with a basally wide costal area due to sinuous course of parallel Sc and R_1; discoidal cell absent, discal area vein-free due to absence of base of R_{2+3}; M unbranched, stem fused with M-Cu_1 cross-vein; Cu_2 reduced.

Genitalia with tenth tergum fused with ninth, forming a blunt median process; preanal appendages long, prominent; aedeagus simple with a pair of strong spines (parameres: Barnard's titillators) lying just above it; clasper stout, spatulate, with subapical indentation, long internal branch and small uncinate spine (Barnard's uncinate titillator); ninth sternum produced.

Female imago

Like male but antennae shorter than body and more slender.

Fore wings with slight differences in bases of anal veins. Hind wings differ in that M is 2-branched, stem present, normal, as is Cu_2 which reaches wing margin.

Genitalia with terminal tergum with apical projection; supragenital plate and vulvar scale(s) present (hard to distinguish); sternites obliquely corrugated; no appendages.

Larva, pupa and their cases

See under family diagnosis and under individual species.

Distribution

South Africa, Cape Province.

Petrothrincus circularis Barnard
(Figs 33-63)

Petrothrincus circularis Barnard 1934: 325, figs 17a-m, 18a-f, r, (male, female, larval and pupal parts, larval case); Scott 1985: 331, fig. q.; Scott 1986: 236; Harrison and Elsworth 1958: 181, table 16, as Molannidae; Harrison 1958a: 260, as Molannidae; Harrison 1958b: 311, table 65.

Lectotype male here selected and designated from Barnard's syntypes, South African Museum, Cape Town.

Type locality: western Cape Province, Table Mountain, Echo Valley, Cape Town, [3318 CD] (named by Barnard as the Type locality, being the only place at which imagos were found.)

In regard to his choice of *P. circularis* as the type-species rather than *P. triangularis* (Hagen), Barnard (1934: 325) comments as follows: "Although by rights *triangularis* Hagen should be made the genotype, I have no adults from the type locality (Swellendam), and the true *triangularis* may possibly, though not probably, prove to be different from the Great Winterhoek specimens which I am describing as Hagen's species. In that case the Great Winterhoek specimens would require a new name. I therefore make *circularis* the genotype". Hagen described his species from larval cases only (Hagen 1864; 225), as *Molanna triangularis.*

Barnard treated his specimens of *circularis* as syntypes. Many are missing. From those that remain the best available male has been selected and marked Lectotype by the present author. This specimen is in spirit. It is the only male with complete antennae and has all other parts present except for one hind leg. The other extant specimens mentioned in Barnard's paper are regarded as Paralectotypes. All specimens are faded and damaged. The extant material and original records are listed after the descriptions of the different stages of *circularis.*

Description of imagos (Figs 33-46).

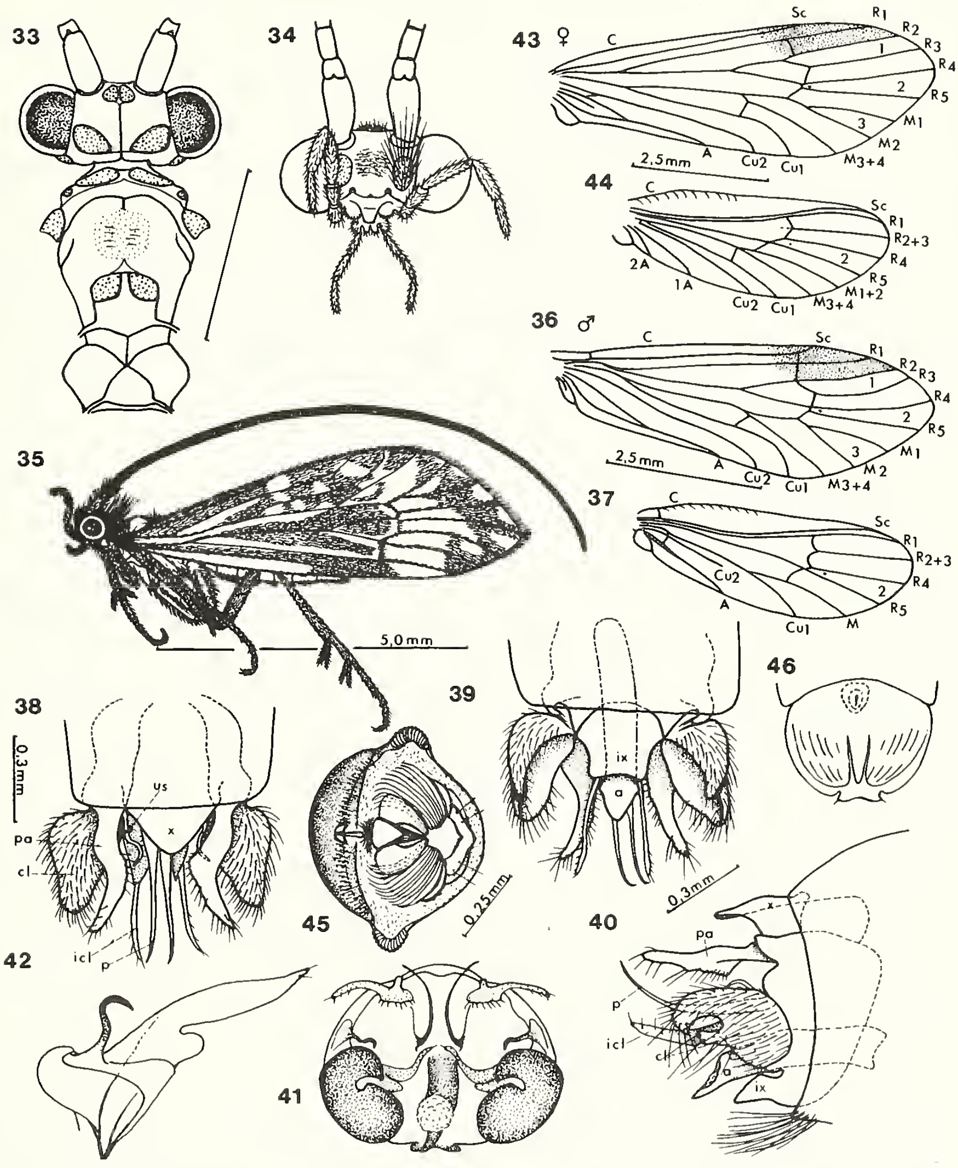
Description of male, female imagos as in generic diagnosis, with the following additional notes made from the imagos, pinned and in spirit, from Barnard's collection, material in the Albany Museum collection, and checked against fresh material received from Dr H. Malicky in 1988 (MISC 311e-j), from which Figs 41, 42 and 45 were drawn. New material (in spirit) appears dusky grey.

Male imago (Figs 33-42)

Small, fore wings 4.8-6.5 mm in length.

Colour, probably of fresh material, described by Barnard (1934: 325) as follows: "Head and thorax fuscous with silvery-white hairs. Legs and palps grey. Antennae dark brown. Wings grey-brown, fore-wing with silvery-white hairs in patches .... [as indicated in Fig. 35]. Abdomen orange-fulvous, the tergites and sternites darker brown." In old pinned specimens the wings appear faded golden brown mottled with pale silvery patches.

Ocelli absent; eyes large, glabrous; vertex with warts all bearing very long setae; mid-cranial sulcus complete; face with a pair of lateral warts bearing long setae and paired mesal patches of short white setae. Antennae stout about a third longer than fore wings; scape stout with long setae, nearly length of head; flagellum finely pubescent, tapered. Maxillary palps (Fig. 34) of median length,



Figs. 33-46. PETROTHRINCIDAE: *Petrothrincus circularis* Barnard, male, female (Scale lines = 1 mm unless otherwise indicated). Material used: KHB (Echo Valley), MISC 311h (Female)

33. male: head and thoracic nota, dorsal. 34. male face, showing maxillary and labial palps. 35. male: entire insect, brownish setae indicated, spaces on wings filled with white setae. 36, 37. male: fore and hind wings. 38, 39, 40, 41. male: genitalia, dorsal, ventral and lateral views, stylized sketch of caudal view showing relative positions of parts (a - aedeagus, cl - clasper, ic/icl - internal branch of clasper, p - paramere, pa - preanal appendage, us - uncinate spine, x - hood formed by tenth tergum). 42. male: inner process of clasper and uncinate spine drawn under compound microscope x 400. 43, 44. female: fore and hind wings (after Barnard 1934, fig. 17a). 45. female: genitalia, end view from new material. 46. female, ventral view (after Barnard 1934, fig. 18f, probably actually a caudal view - dorsal and ventral views do not show vulvar scale etc.).

densely pubescent, 5-segmented, carried upwards over face; two basal segments short, rest subequal but third longest and fifth shortest, simple. Labial palps (Fig. 34) 3-segmented, with segments subequal; third segment simple, finely pubescent.

Pronotum narrow, with median pair of warts long, lateral pair small, round, hard to see unless long setae are still present (they are easily lost); mesonotum with a quadrate median area bearing recumbent white setae; scutellum with warts bearing long setae. Legs hairy; middle and hind tibiae with a few colourless spinelike setae, no black ones. Wings (Figs 35-37) with venation as in generic description and as illustrated in the figures.

Genitalia (Figs 38-42) with terminal tergum triangular; preanal appendages large, curved, with median expansion, distally curved outward and upward; aedeagus simple with narrow apex and subapical membranous area with a pair of long parameres arising just above it; paired strongly spatulate claspers each with a long inner branch with basal expansion and small simple uncinate spine (Figs 41 and 42); apex of clasper bifid; ninth sternum apically truncate, slightly indented.

Female imago (Figs 43-46)

Similar to male in coloration and general appearance but slightly larger, fore wings 5.4-7.5 mm long.

Antennae shorter than in male, slender.

Fore wings practically identical to those of male except for basal parts of anal veins; hind wings show considerable differences. Hind wings with M two-branched, joins Cu_1 at base; Cu_1 simple, Cu_2 complete, anals separate (Fig. 44 compare with Fig. 37). Hind wings have a large patch of blackish hairs on the lower surface; these tend to stick to the egg mass when laid.

Genitalia (Figs 45, 46) having terminal terga (ninth + tenth) with dorsal projection the shape of which depends entirely on angle of viewing; as in Fig. 45, 46 or 72 (of *triangularis*). Sternites membranous, showing lightly sclerotized ridges resembling pleural folds; single median vulvar scale, presumably covering vulvar opening, lateral to which the supragenital plates can be seen. Vagina clearly visible.

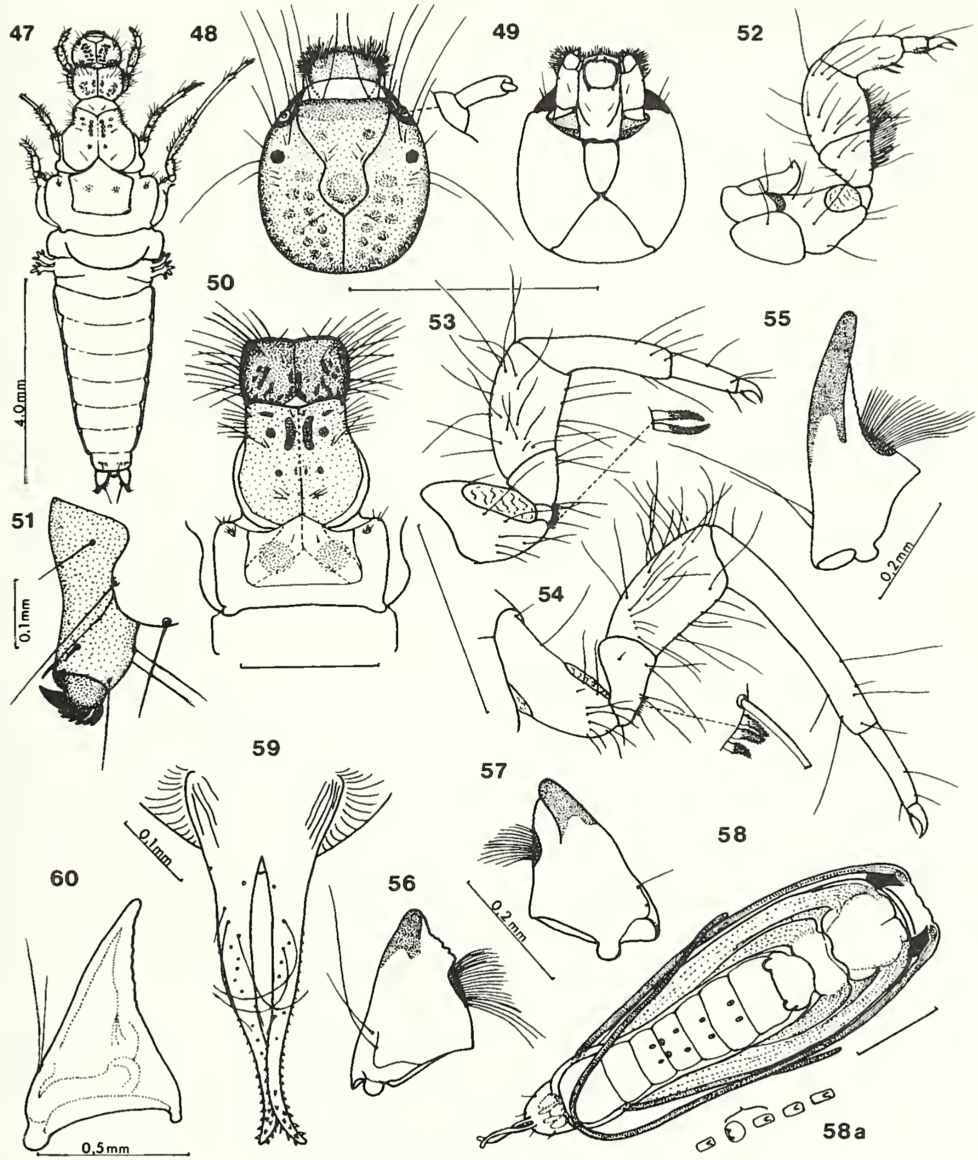
No good adult female of Barnard's material was available for comparison with his drawings, of which his Fig. 18 f. has been reproduced here as Fig. 46. There is, however, a good female pupa, which coincides well with them. The genitalia of one of the two females collected by Dr Malicky have been cleared and drawn (Fig. 45) for comparison with those of *P. triangularis* (Figs 68, 72). See also the SEMs of *P. demoori* female genitalia, which help considerably in elucidation (Figs 82-85).

Description of mature larva (Figs 47-57 and 61-63).

The following description and drawings were made from Barnard's own specimens and the more recently collected larvae in the Albany Museum (all material in spirit). Comparisons were made with Barnard's text.

Case dweller; up to 7 mm in length; dorsoventrally flattened; head, thoracic nota and legs light brown to yellowish or pallid in colour, with patterning of brown spots or marks, often faint; abdomen white.

Head (Figs 47-49, 62, 63) hypognathous, rounded; frontoclypeal apotome with single pair of lateral indentations; ventral apotome suboval, completely separating the genae. Eyes situated well forward, each under four cuticular lenses. Antennae small, near mandibular bases. Labrum small,



Figs. 47-60. PETROTHRINCIDAE: *Petrothrincus circularis* Barnard: 47-57. mature larva; 58-60. male pupa.
(Scale lines = 1 mm unless otherwise indicated).
Material used: MISC 291a (Figs 47-57); KHB (Figs 58-60).
47. Habitus of mature larva, dorsal. 48, 49. Head, dorsal and ventral, antenna much enlarged. 50. Thoracic nota, dorsal. 51. Left anal proleg, outer view. 52, 53, 54. Right fore, middle and hind legs, fore leg with pleural sclerites, middle and hind legs with trochanteral setulae further enlarged. 55. Right mandible of newly ecdysed larva, ventral. 56, 57. Right and left mandibles of older larva, ventral. 58. Habitus, dorsal, dorsal plates further enlarged. 59. Anal appendages. ventral, further enlarged. 60. Left mandible, dorsal.

rounded, prominent, with very small, paired indentations. Anteclypeus large, colourless. Labium thick with very small pair of palps. Maxillary palps apically small with large stout bases. Both mandibles with inner brush, in recently ecdysed mature larvae long, with slightly serrated ventral and apical cutting edges and with dorsal edge heavily sclerotized, plain; in older larvae the apical third may be worn away (compare Fig. 55 with Fig. 56), presumably due to grazing on the rock surfaces on which they live.

Thorax (Figs 47, 50) with prosternal horn absent. Pronotum sclerotized, without carina or anterolateral expansions; median suture present, sometimes faint or partial; pattern of muscle spots, often inconspicuous. Mesonotum with a pair of large pale yellow sclerites which may show brownish spots indicating Barnard's "three to four pairs of small chitinous plates medianly"; the median spots tend to run together forming paired median stripes; mesonotal plates shiny and lightly pitted; median ecdysial line faint or partial. Metanotum very broad, widest segment, with small paired posterolateral lobes of unknown function, with possible quadrangular median sclerite, hard to distinguish, shining and lightly pitted, colourless, with pair of vague brownish spots, segment otherwise membranous (this possible sclerite is not usually visible apart from the spots), with paired raised diagonal strips (Fig. 50) apparently overlying paired muscles. Sternum membranous with minute paired ventrolateral extensions of pronotum. Pleural sclerites largely colourless; pre-episternum long, sclerotized, with upturned tip, wide in lateral view, narrow in dorsal view (Fig. 52). Fore legs (Fig. 52) short, stout, with few long setae except on trochanter and femur which have a ventral fringe of long, simple setae; middle legs (Fig. 53) longer; hind legs (Fig. 54) longest; both middle and hind legs slender in dorsal view, wide in lateral view, with long setae but no ventral brushes; middle and hind trochanters with minute setulose marginal spines. Fore claw as long as tarsus, middle and hind claws little longer than fore claw, each with a single seta part way along claw.

Abdomen (Figs 47, 51) with lateral line fringe and lateral tubercles absent; a very narrow lateral fold along each side; segments not indented dorsally though deeply so ventrally (presumably to increase the respiratory surface); several segments with small, stout gills; first segment very broad, with wide flattened dorsal hump and large lateral humps; second segment with three pairs gills of which dorsolateral gills simple or bifid, lateral and ventrolateral ones 3-4 branched; third to fifth segments with a single ventral pair of branched gills; sixth segment with a simple pair; anal prolegs with colourless lateral sclerites and longer than is usual in eruciform larvae, fused only partially, not really forming an apparent tenth segment; anal claws very small with neat dorsal comb of teeth (Fig. 51).

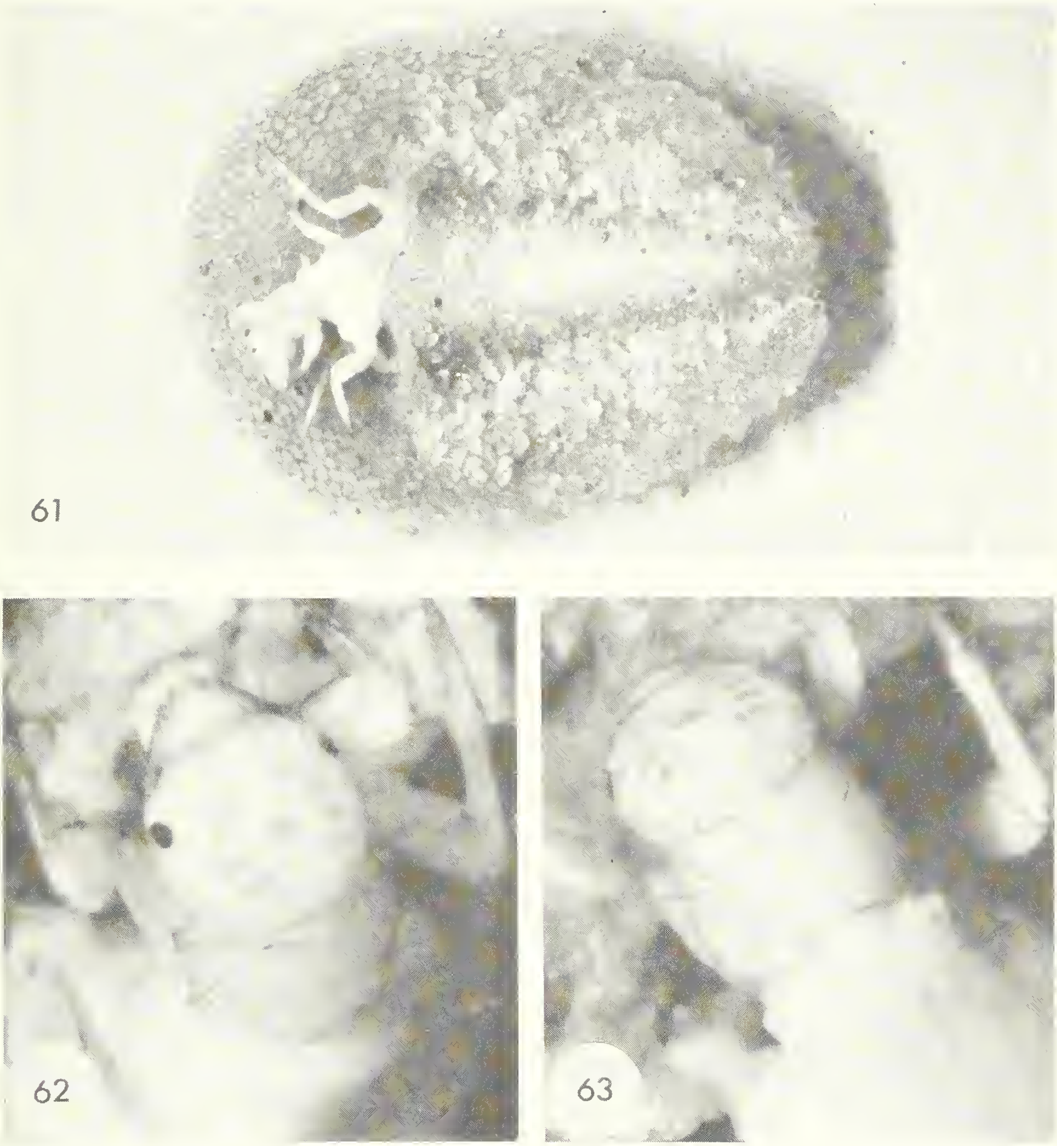
Larval case (Fig. 61)

Limpet-shaped, subcircular, of minute sand grains cemented and lined with silk secretion, with ventral shelf (plastron) of sand grains supporting the larva, the spaces lateral to this being filled in with sand grains loosely held together by secretion, with a small oval posterodorsal aperture. The species name is derived from the subcircular larval case.

DESCRIPTION OF PUPA (Figs 58-60).

Male pupa

Antennae much longer than body, at least one and a half times body length, curled round as shown in Fig. 58. Labrum semicircular. Mandibles strong, triangular, with the apex blunt and with



Figs. 61-63. PETROTHRINCIDAE: *Petrothrincus circularis* Barnard, mature larvae.

61. Photograph of mature larva in case, ventral. 62. Photograph of head of larva, frontal view, further enlarged. 63. Photograph of head and thorax of larva, dorsal, further enlarged. Photographs by J.C. Hodges, Jr. (Ex MISC 291a).

inner margin feebly serrated. Fore and middle tarsi fringed for swimming. Lateral fringe and gills absent. Wing sheaths reaching end of segment 7. Segment 1 with a small pair of posterolateral lappets; segments 3-6 with small presegmental dorsal plates each with one tooth and segment 5 with in addition postsegmental dorsal plates each with two teeth (Figs 58, 58a). Anal appendages slender, slightly wrinkled, with a few long setae and many small blade-like bristles, particularly apically. No special pocket for male genitalia.

Female pupa

Similar to male but tends to be larger; antennae shorter, ends curled, meeting ventrally about segment 7 or 8.

Pupal case

The larval case is utilized, being sealed down onto a rock or stone round the margin. The larva spins a transparent ventral membrane sealing off the front end anterior to the plastron. Emergence is through a semicircular anterodorsal aperture in the case, cut by the pupal mandibles at eclosion.

DISTRIBUTION

South Africa, high mountain streams in the coastal ranges in the Cape Province, mainly in the western Cape, but also in the southern Cape. There is also a single isolated record from the vicinity of Rhodes in the Witteberg Mountains, southern outliers of the Drakensberg, eastern Cape Province (Jacquemart 1963), but this may prove not to be of *P. circularis,* as only larvae were collected, and the larval cases are very similar to those of *P. demoori.*

MATERIAL EXAMINED

South African Museum material

Pinned material

Paralectotypes: Echo Valley, Table Mountain, Cape Town [3318 CD] [2 990 ft = 911 m] (KHB, February-April 1933, 5 males in fair condition, one lacks two wings, one lacks one wing and abdomen, antennae are broken or missing and most palps are damaged or lacking, 9 females in fairly good to very poor condition, two lack genitalia).

Material in spirit

Lectotype: Echo Valley, Table Mountain, Cape Town [3318 CD] [2 990 ft = 911 m] (KHB, February-April 1933, male).

Paralectotypes: Echo Valley, Table Mountain, Cape Town [3318 CD] [2 990 ft = 911 m] (KHB, February-April 1933, 7 males in good to poor condition, bits of others and a cleared male abdomen, a single female body with thorax, legs and genitalia, the latter badly damaged).

Other material: Echo Valley, Table Mountain, Cape Town [3318 CD] [2 990 ft = 911 m] (KHB, February-April 1933, 3 immature pupae and larval and pupal exuviae); Hottentots Holland Mountains, [3418 BB] 4 000ft [= 1 219 m] East side (KHB, January 1933, larvae and pupae in cases).

Albany Museum material

Material in spirit

Western Cape Province: Great Berg River, French Hoek [Franschhoek] Forest Reserve, main stream [3319 CC] (MISC 288: KMFS, 30.i.76, larvae); Assegaibos tributary [3319 CC] (GBG 131b: ADH, 30.x.1950, larvae); same place (MISC 289: KMFS, 30.i.76, larvae). Riviersonderend, French Hoek [Franschhoek] Pass [3319 CC] (MISC 290: KMFS, i and ii.1976, larvae); Witte River, Wolwekloof tributary [3319 CA] (MISC 291: KMFS, i and ii.1976, larvae); Breede River, Elandspad tributary [3319 CA] (MISC 292: KMFS, i and ii.1976, larvae); Witte River, Bastiaanskloof tributary [3319 CA] (MISC 295c: KMFS, i and ii.1976, larvae); Langrivier, main stream (MISC 297a: KMFS, i and ii.1976, larvae) and Assegaibos stream (MISC 298d: KMFS, i and ii.1976, larvae), both tributaries of the Eersterivier [3318 DD]); Witte River, Happy Valley [3319 CA] (MISC 304a: KMFS, i and ii.1976, larvae) ; Langrivier [3318 DD] (JMK, iii.75, larvae and pupa, vi.83, larva, x.83, 2 larvae, xi.83, 2 larvae); small feeder streams of the Dutoitsrivier in the Mount Rochelle Nature Reserve, Franschhoek Pass [3319 CC], at 900-1 000 m altitude (MISC 311 e-g, and h and j, HM, 20.iii.88, 3 male imagos and 2 female imagos, at light).

MATERIAL CITED IN LITERATURE

Barnard 1934: 325. Type locality: Table Mt. Cape Town [3318 CD] (KHB February - April, males, females). Groot Drakenstein (ACH); Jonkershoek, Stellenbosch [3318 DD] (KHB and HGW); Witte River, Wellington Mts [3319 CA] (KHB, November 1922); River Zonder End Mts [3319 AB] (HGW); Palmiet River [3418 BD] (HGW); Hottentots Holland Mts [3418 BB] (KHB); Great Winterhoek Mts (KHB and HGW); French Hoek [Franschhoek] Mts [3319 CC] (KHB and HGW); Elands Kloof, Citrusdal [3219 CA] (HGW).

These localities are all in the western Cape coastal folded belt. Contrary to his usual custom, Barnard did not give dates under each entry; these do appear on the labels with the specimens, but where specimens are missing there is now no possibility of dating them. The extant material is listed above under material examined.

All the records, apart from the Table Mountain and Hottentots Holland specimens were evidently of larvae only. The Hottentots Holland material also included many pupae, unfortunately immature.

Jacquemart (1963): western Cape Province: near Hermanus [3419 AC], twin waterfalls on Maanschijnkop (21.xii.1950, larvae); at Hermanus [3419 AC], stream (22.xii.1950, larvae); near Grabouw [3419 AA], Viljoenspas (11.ii.1951, larvae). Eastern Cape Province: 5 miles E.N.E. Rhodes [3027 DC], (on Witteberg Mountain, an outlier of southern Drakensberg Mountains), high mountain stream (10.iii.1951, larvae). The larvae from the eastern Cape may prove not to be of *circularis*, when male imagos are available. A recent search of the area by Dr F.C. de Moor and Miss H.M. Barber failed to discover any, but a further search will be made, as it is important to know if it is indeed *circularis* or *demoori* or another species.

***Petrothrincus triangularis* (Hagen)**
(Figs 64-73)

Molanna triangularis Hagen 1864: 225 (larval case only).

Petrothrincus triangularis (Hagen), Barnard 1934: 325, 327, figs 18g-q (male, female, case); Barnard 1940: 643 (cases); Harrison 1958a: 260.

Neotype male here selected and designated from Malicky's specimens, Albany Museum, Grahamstown.

Type locality: Swellendam, western Cape Province [3420 BB].

Neotype locality: Dutoitsrivier in Mount Rochelle Nature Reserve, Franschhoek Pass, western Cape.

The name, *Molanna triangularis* Hagen 1869, was validly published in spite of the fact that the only material available to Hagen was an empty larval case because to satisfy the provisions of the International Code of Zoological Nomenclature (1985) a name published before 1931 need only be based on an "indication", in this instance "the description of the work of an extant animal" (Criteria of Availability, Article 12). The Type specimen, an empty larval case, is presumed lost.

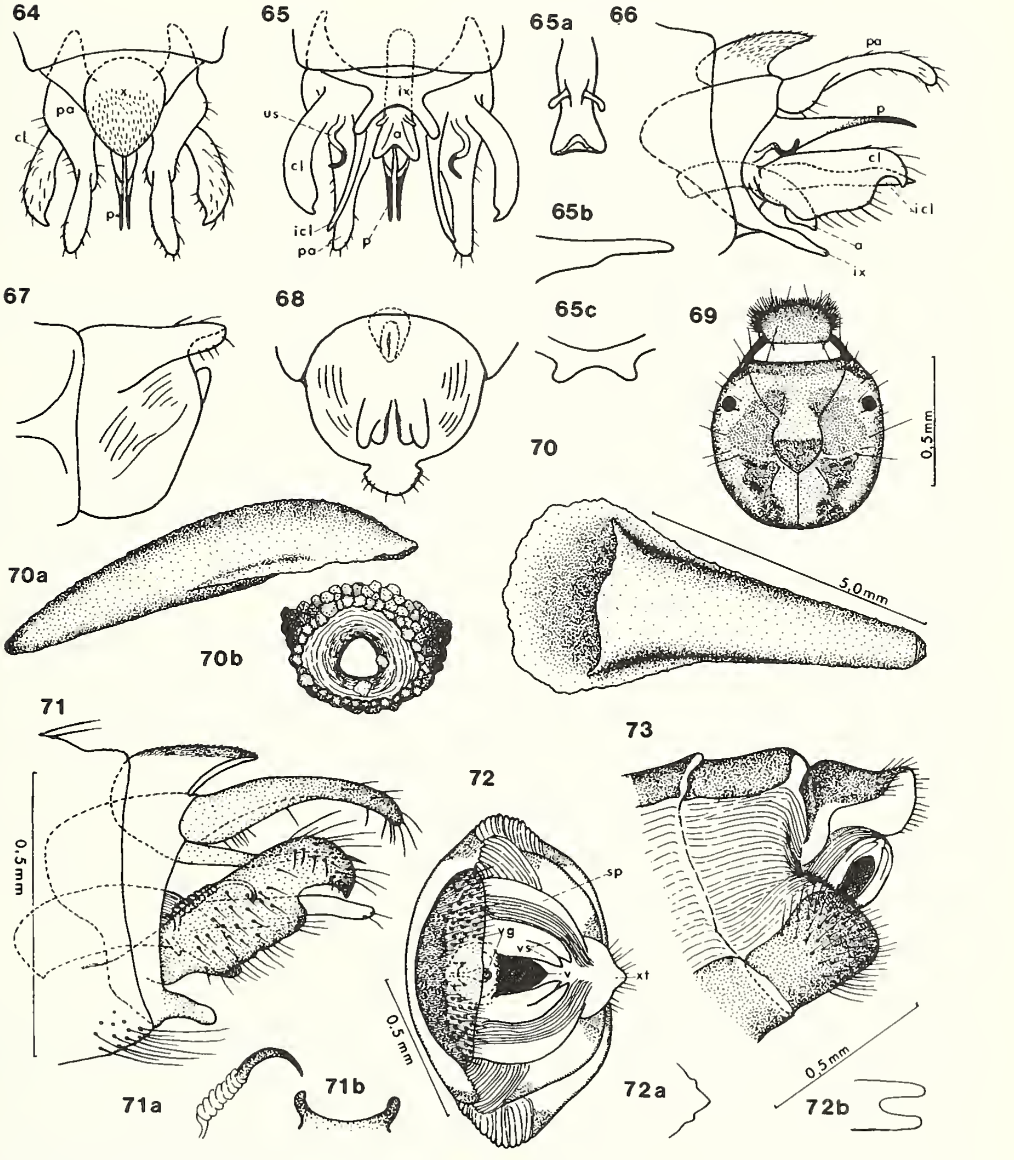
As Hagen had no imagos Barnard described them from his own material but, as was his wont, did not designate a type. Barnard's extant material and original records are listed after the descriptions of the different stages. The extant male lacks its genitalia and so cannot be named a Neotype. Two males and two females were received recently from Dr H. Malicky. These were collected at light, together with *circularis* imagos, from small feeder streams of the Dutoitsrivier in the Mount Rochelle Nature Reserve, Franschhoek Pass, western Cape [3319 CC], at 900-1 000 m altitude. The best male (MISC 311a) is here designated the Neotype. It is lodged in the Albany Museum.

DESCRIPTION OF IMAGOS

Imagos (Figs 64-68, 71-73)

According to Barnard (1934) the coloration of the imagos and the wing venation are as in *circularis*, excepting that the fore wings appear to have more patches of silvery white setae, and the setal fringes are very long, particularly on the anal margin of the hind wings. (Setae fringing wings in *circularis* may be equally long but may have been lost or abraded in the extant material.) The recent light trap specimens have, unfortunately, lost most of their setae, including wing fringes. The length of the male fore wings is 5.5-6.8 mm and that of the female is 6.0-7.9 mm. The descriptions are based on Barnard's descriptions and drawings and remaining female imagos and upon the material collected by Malicky. There are very minor differences in wing venation between *triangularis* and *circularis*, not sufficient to affect the generic diagnosis or even to differentiate between the species in the absence of genitalia.

The male genitalia (Figs 64-66, 71) are compared with those of *circularis* (Figs 38 - 42). They have the ninth tergum ovate not triangular; preanal appendages longer and wider, curved in lateral view, lacking the median expansion, but with a small basal expansion; aedeagus with apex indented, and two small sclerotized ventral processes (Fig. 65a), the parameres are shorter and stouter with



Figs. 64-73. PETROTHRINCIDAE: *Petrothrincus triangularis* (Hagen), male, female, larva
(Scale lines = 1 mm unless otherwise indicated).
Material used: MISC 311b (male), MISC 311 c and d, and KHB (female), MISC 290b and KHB (larva), King 31 (case).
64-66. Male: genitalia, dorsal, ventral and lateral views. 65a; Ventral view of aedeagus. b, c; variations in shape of spine (titillator) and ninth sternite. 67, 68. female: genitalia, lateral and ventral views. 69. Mature larva: head, dorsal. 70, 70a. Larval case: ventral and lateral views. 70b, posterodorsal end of case to show membrane in which distal opening lies. (Figs 64-68 after Barnard 1934, figs 18 g-n.) 71-73. Drawings made from new material of *P. triangularis*. 71. Male: genitalia, lateral (compare with Fig. 66); 71a. Uncinate process (x 400); 71b. Ninth sternite. 72,73. Female: genitalia, caudal and skewed lateral views; 72a. Variation in shape of tergite. 72b. Supra- genital plate (not to same scale). (a - aedeagus, cl - clasper, ic/icl - internal branch of clasper, p - paramere, pa - preanal appendage, sp - supragenital plate, v - vulva, vg - vagina, vs- vulvar scale, x - hood formed by tenth tergum xt - tenth tergum)

straight apices and wide bases. The claspers are spatulate but longer and basally narrower in lateral view, their internal processes longer, the uncinate spines larger, with basal part apparently coiled like a spring (Fig. 71a). The ninth sternum is widely bifurcate with the arms varying in size (compare Figs 65, 65c, 71, 71b).

The female genitalia (Figs 67, 68, 72, 73) are compared with those of *circularis* (Figs 45, 46). They have the terminal dorsal projection stronger, sub-ovate to subtriangular, not apically indented; paired lateral vulvar scales, each bifid; large median vulvar opening, clearly visible. The supra genital plate is transparent, narrowly bifurcate (Fig. 72b). The vagina is small, sternites apparently showing lightly sclerotized pleural folds.

Setae under hind wings of female are pale, not blackish as in *circularis.*

In comparing Fig. 72 (*triangularis*) with Fig. 45 (*circularis*) note that the scale is the same, but one is a very large individual, the other very small. Although *triangularis* is the larger species, the difference in size range is not great.

DESCRIPTION OF LARVA (Figs 69-70)

The larvae fit tightly into their cases and are therefore difficult to extract and as a result their abdomens are frequently not well preserved. The best available larvae (collected from the Langrivier (W Cape) by Dr J.M. King) are those which were preserved in Kahle's fluid immediately after collection but even in these the metanotum and some sterna are poorly preserved and their structure unclear, as are the gills.

The largest available larvae are 6-7 mm in length.

The larva (Fig. 69) is as in *circularis* but the sclerotized parts are more strongly coloured and easier to see, the colour pattern is clearly distinguishable, somewhat different from that in *circularis* (compare Fig. 69 with Fig. 48). In Barnard's material the head and pronotum are brown with faint patterning. In fresh specimens the head shows strong markings similar in type to those in *circularis* but the spots lateral to the frontoclypeal apotome are confluent and the central spots larger and bolder. The mandibles, as in *circularis,* are long in newly ecdysed specimens and worn down in older ones (compare with Figs 55-57). The thoracic nota also show minor differences in patterning. The pronotum has a clear median division and the mesonotal plates are also clearer, as is the metanotum. The larvae do not show a possible metanotal sclerite. No branched abdominal gills were found, but a single pair of simple ventral gills is present on segments 2-6.

Larval case

The larval case (Figs 70, 70a, 70b) is similar in type to that of *circularis,* but is narrowly triangular in shape, giving rise to the specific name. The sides are nearly straight, the tube wide, round, and the posterodorsal aperture has a central opening in the terminal membrane (Fig. 70b), in some instances on a small chimney. Barnard's drawings of the case must have been made from an unusual specimen, as an incorrect impression is given of the lateral flanges. The case has therefore been re-drawn after comparison with Barnard's original material and the Albany Museum specimens of which there are many.

Description of pupa

The pupae like the larvae fit tightly into their cases and are therefore difficult to extract and as a result their abdomens are frequently not well preserved.

The pupa is similar to that of *circularis*. The case is similarly attached to the substratum and widely opened anterodorsally by the pupal mandibles when the pharate imago emerges.

Distribution

South Africa, western and southwestern Cape.

Material examined

South African Museum material

Pinned material

Western Cape: Great Winterhoek Mountains, 4 000 ft. [= 1 219 m] [3319 AC] (KHB and HGW, iii.1933, 1 male without genitalia, 2 females).

Material in spirit

Western Cape: Great Winterhoek Mountains, 4 000 ft. [= 1 219 m] [3319 AC] (KHB and HGW,i.1933, 10 larvae in cases, 47 immature pupae, most in cases).

Albany Museum material

Material in spirit

Neotype: western Cape: feeder streams of the Dutoitsrivier, Franschhoek Pass (3319 CC) (MISC 311a: HM, 20.iii.1988, male, to light)

Other material: western Cape: Great Berg River, Assegaibos main stream [3319 CC] (GBG 40c: ADH, 2.viii.1950, larvae); Great Berg River, source, 3 500 ft [= 1 067 m] [3319 CC] (GBG 134e: ADH, 21.xi.1950, larvae); same, 3 000 ft [= 914 m] (GBG 134e: ADH, 21.xi.1950, larvae); Upper Langrivier, tributary of Eerste Rivier [3318 DD] (JMK, iv.1975, 1 pupa; iv-xi.1984, many larvae, and in iv and v. 1975, empty pupal cases); Riviersonderend, French Hoek [Franschhoek] Pass [3319 CC] (MISC 290b: KMFS, 30.i.1976, larvae); feeder streams of the Dutoitsrivier, Franschhoek Pass (3319 CC) (MISC 311b-d: HM, 20.iii.1988, 1 male and 2 females, to light). South western Cape: Vetrivier tributary high on Garcia's Pass, [3321 CC] (MISC 306K: KMFS, 9.ii.1976, larvae).

Material cited in literature

Hagen 1864: 225. Swellendam [3420 BB] (larval case) (as *Molanna triangularis* Hagen).

Barnard 1934: 325. Swellendam (Hagen, case only); Great Winterhoek Mts., Tulbagh (KHB and HGW, November 1932, larvae, males and females bred out March 1933); Jonkershoek, Stellenbosch [3318 DD] (HGW); Witte River, Wellington Mts [3319 CA] (KHB, 1922); Bain's Kloof, Wellington

Mts (KHB and HGW, 1 May 1933, females); Hottentots Holland Mts (KHB and HGW, 1932); Du Toit's Kloof, Rawsonville (KHB, 1932); Mostert's Hoek and Waai Hoek Mts [3319 AD] (KHB, April 1933); Bosch Kloof, Keeromberg, [3319 DA], Worcester (KHB, 1930); Cedar Mts, Clanwilliam [3219 AC] (KHB, 1930); French Hoek [Franschhoek] Mts [3319 CC] (KHB and HGW, 1932).

Barnard 1940: 643, Valsch Gat stream on Ceres side of Matroosberg, Hex River Mts, western Cape [3319 BD] (KHB, November 1933, empty cases).

The extant material is listed above under material examined. The only adults Barnard had were males and females bred out from larvae and pupae collected on the Great Winterhoek Mountains at 4 000 ft. [= 1 219 m] [3319 AC]. Of those only two females remain. One is complete and in good condition, with an egg mass adhering to and distorting the apex of the abdomen. One antenna is unbroken. It is almost as long as in the newly collected males. The other female has lost two wings and the abdomen.

Petrothrincus demoori sp. nov.
(Figs 74-85)

Holotype male (SCR 4A) here selected and designated, from material in the Albany Museum.

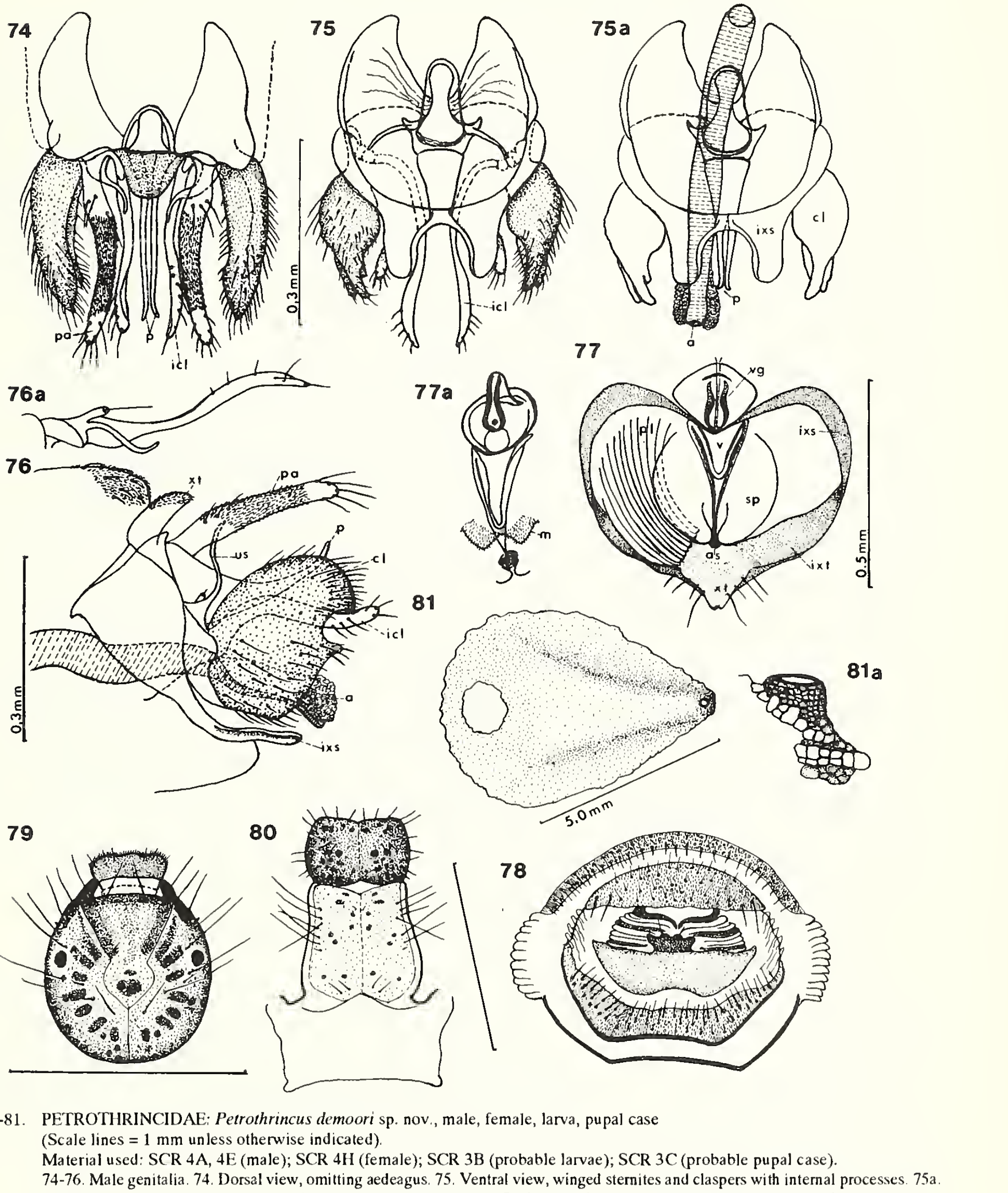
Type locality: southern Cape, Plaat River, tributary of the Karatara River, at Klein Plaat se Brug (33°53'20"S, 22°50'45"E, altitude *c* 280 m.

Ten male and six female imagos collected using a light trap at the type locality and putative pupae (SCR 2A and 3C) and putative larvae (SCR 3B) collected from Jubilee Creek, a tributary of the Homtini River (all by Dr F.C. de Moor and Miss H.M. Barber) were at first thought to be *P. circularis* on account of their subcircular larval cases. Both streams are in the same general area in the southern Cape nowhere near the habitats of the two hitherto known species of *Petrothrincus*. On examination the males proved to be a new species of *Petrothrincus*. The larval cases are subovate rather than subcircular (Fig. 81) but there is certainly an overlap between the cases of the two species. The species is named after Dr de Moor.

After study of the specimens, a Holotype male (SCR 4A) was selected and designated by the author. The remaining nine males (SCR 4B, C, D and 4E with 6 males) were designated Paratypes, as were the six females (SCR 4F, 4G - used for S.E.M. micrographs - and 4H with 4 females). The Holotype and the Paratype males and four of the Paratype females are all lodged in the Albany Museum. The remaining two Paratype females were sent to Dr A. Neboiss, Museum of Victoria, Melbourne, Australia.

Description of imagos (Figs 74-78, 82-85)

The adults are somewhat teneral and in spirit. They are very similar in general appearance to *circularis* and *triangularis:* small, dusky grey insects, length of fore wings 5.4-6.0 mm in males, 5.8-6.8 mm in females. The wings show little trace of lighter and darker patches but this may be due to the teneral nature of the material. The wing venation is very like that in the other two species with a few very minor differences that do not affect the generic diagnosis. In the fore wings, there are, however, long hyaline streaks along the R_3+M cross-vein, the base of the R_{4+5} fork and the adjacent part of the lower margin of the discoidal cell, also along M for almost the whole length of the thyridial cell. Such hyaline streaks were not seen in the other two species. Some cross-veins in the hind wings



Figs. 74-81. PETROTHRINCIDAE: *Petrothrincus demoori* sp. nov., male, female, larva, pupal case (Scale lines = 1 mm unless otherwise indicated).
Material used: SCR 4A, 4E (male); SCR 4H (female); SCR 3B (probable larvae); SCR 3C (probable pupal case).
74-76. Male genitalia. 74. Dorsal view, omitting aedeagus. 75. Ventral view, winged sternites and claspers with internal processes. 75a. Same: sternites and aedeagus (broken lines), parameres and claspers. 76. Lateral view: preanal appendage, clasper and internal process, uncinate spine, parameres, aedeagus and left side of sternite. 76a. Internal process and uncinate spine further enlarged. 77,78. Female genitalia. 77. Caudal view, showing sclerotized ring, supragenital plates, vaginal apparatus, etc. 77a. Vaginal process raised up; also setulose membranous covering, shown as seen. 78. Sketch of genitalia as seen in end view; note sclerotized pleural folds resembling a pile of saucers. 79, 80. Larva. 79. Head, dorsal. 80. Thorax, dorsal. 81. Pupal case showing opening left by pharate imago after eclosion. 81a. Lateral view of chimney-like posterior aperture of case. (a - aedeagus, cl - clasper, ic/icl - internal branch of clasper, ixs - ninth sternite, ixt - ninth tergum, m - setose membrane, p - paramere, pa - preanal appendage, pl - pleura, sp - supragenital plate, us - uncinate plate, v - vulva, vg - vagina, x - hood formed by tenth tergum xt - tenth tergum)

are faint, but both these facts could be due to the teneral nature of the material.

Male genitalia (Figs 74-76) are in general typically petrothrincid. They differ from those of the other species as indicated below. Preanal appendages lack both the median expansion of *circularis* and the basal one of *triangularis,* and are not strongly angled; they are minutely setulate. Parameres are basally broad, not narrow, in lateral view (Fig. 76). Claspers are more broadly quadrangular than in either of the other species, with the apical excision small; left and right claspers are very similar, whereas in *circularis* one is larger than the other. The internal process of the clasper is much like that of *triangularis* but the uncinate spine resembles that of *circularis* excepting that it has an additional basal process tipped with a small seta (compare Figs 42 and 71a with Fig. 76a). The aedeagus is very long with a lengthy narrowed apical section bearing a membranous expansion (Fig. 76). The lateral processes of the ninth sternum are strongly winged unlike those of the other two species (Figs 75, 75a).

Female genitalia (Figs 77, 78, 82-85), as might be expected, are very similar in general type to those of *circularis* and *triangularis.* As in those species, they are best seen in caudal view.

The dorsal process and vulva resemble those of *triangularis*, but the lateral striated areas are wider and there appear to be paired vulvar scales (Fig. 84). In caudal view (Fig. 78) these striated areas resemble a pile of saucers. The dorsal process is lightly sclerotized dorsally and this sclerotization extends laterally, embracing the sides of the genitalia (Fig. 77) as in *triangularis.* There is a broad, apically bifid supragenital plate and the ninth tergum and sternum together form a sclerotized ring (Fig. 77). The vagina is hour-glass shaped.

The species are not easily distinguished from one another unless cleared and checked against the figures (compare Figs 45, 72 and 77).

The female supragenital plate was first clearly seen in this species (Fig. 77) (its appearance differs when seen at different angles) and was then found in *triangularis* (Fig. 72b) and in *circularis* (Fig. 45). Scanning electron micrographs of the female genitalia (Figs 82-85) shed further light on the structures. There is an apparently lightly sclerotized, bilobed setose membrane, shown in Fig. 77a, the function of which is unclear. As seen, it lies above everything else, being very clear in Figs 82-85. Also very clear are the ridges on the supragenital plate, and what appear to be the paired vulvar scales (Fig. 84) between the arms of the supragenital plate and the membranous lobe, which is actually ventral to them.

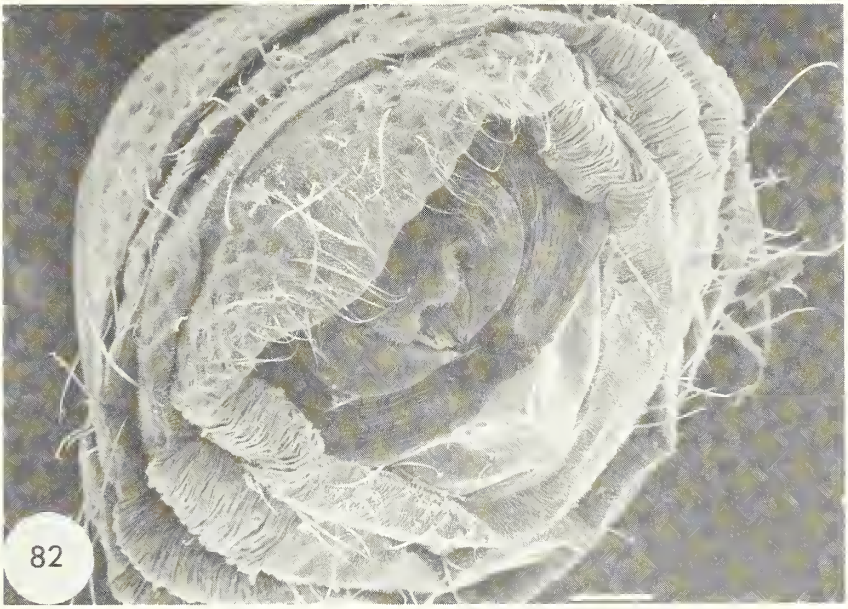
DESCRIPTION OF PUTATIVE LARVA (based on the three available larvae in cases, SCR 3B) (Figs 79, 80,).

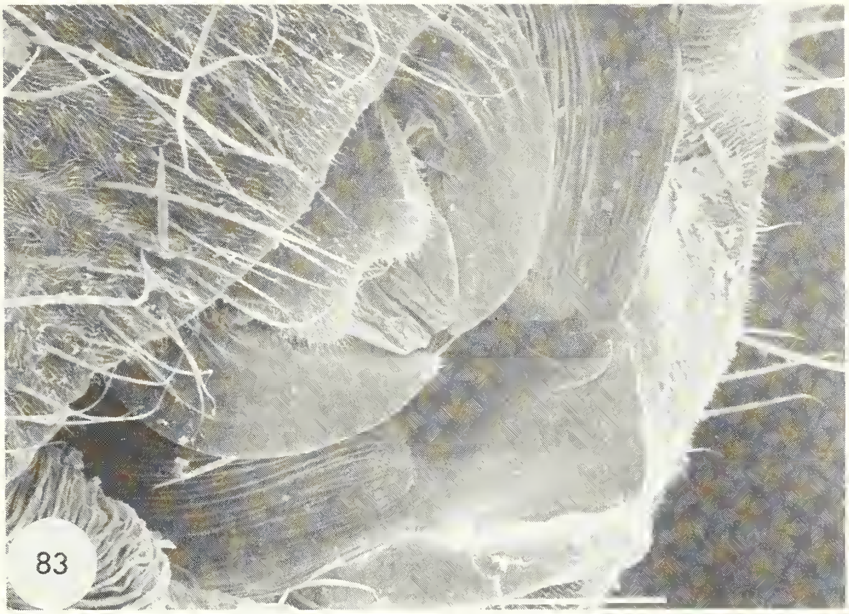
Length of mature larva 6.0 - 6.6 mm.

The head pattern (Fig. 79) is of the same type as that of *circularis,* though the frontoclypeal pattern is nearer that of *triangularis* (compare Figs 48, 69 and 79). The pattern on the pronotum shows many more spots than in *circularis;* the mesonotum is very pale, showing a few very small spots, the mid-line is clearly visible; the metanotum is entirely membranous. Abdominal gills resemble those of *circularis* but have longer branches. There are three pairs on the second abdominal segment (2-4-branched), two pairs on the third (2-branched) and one pair each on the fourth and the fifth (2-branched).

Larval case

Length of case 6.5 - 7.5 mm; sub-ovate, similar to that of *circularis* but on average narrower relative to length. There is a definite overlap in size and shape between the two species. The larval





Figs. 82-83. PETROTHRINCIDAE: *Petrothrincus demoori* sp. nov., female.
Material used: SCR 4G (subsequently lost).
82. Female genitalia, caudal view. Scale line 100 μm. Seen in situ with sternites, terga and pleura surrounding it. 83. Same. Scale line 100 μm. Note apex of tergum X on right, supra genital plates, and between them, vulvar scales; above them setose membrane.

case is exactly like the pupal case except for the absence of the neat escape aperture (Fig. 81).

DESCRIPTION OF PUTATIVE PUPA (SCR 3C, 17 pupae).

The available pupae, all apparently still immature, resemble those of the other two species.

Pupal case (Fig. 81)

An empty pupal case is figured (Fig. 81) to indicate the size and position of the escape aperture which is much neater than in *triangularis* in which the openings are evidently torn, not cut, leaving a ragged hole with upstanding lateral flaps. The posterior opening is also figured (Fig. 81a) showing the turret. In pupal cases the turret is filled with sand grains (not shown), whereas in the larval case it is open. A turret is not always present.

DISTRIBUTION

South Africa, mountain streams in the coastal range of the southern Cape. The original estuaries and lower reaches of the rivers in this region have been drowned so that the present estuaries are preceded by what was originally the middle or upper reaches of the rivers. Consequently the present altiitudes of the tributaries are lower than they will originally have been.

MATERIAL EXAMINED

Albany Museum material

Material in spirit

Holotype: Southern Cape Province: Plaat River, tributary of the Karatara River, at Klein Plaat se Brug (33°53'20"S, 22°50'45"E), altitude *c* 280m (SCR 4A: FCdM and HMB, 7-8.iii.1989, male).

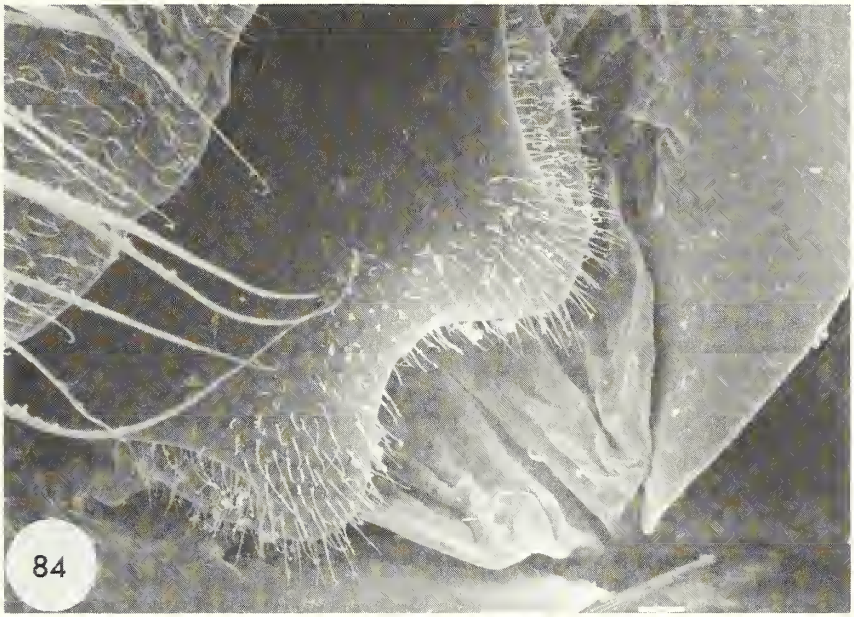
Paratypes: Southern Cape Province: Plaat River, tributary of the Karatara River, at Klein Plaat se Brug (33°53'20"S, 22°50'45"E), altitude *c* 280m (SCR 4B-H: FCdM and HMB, 7-8.iii.1989, 9 male and 4 female imagos, to light).

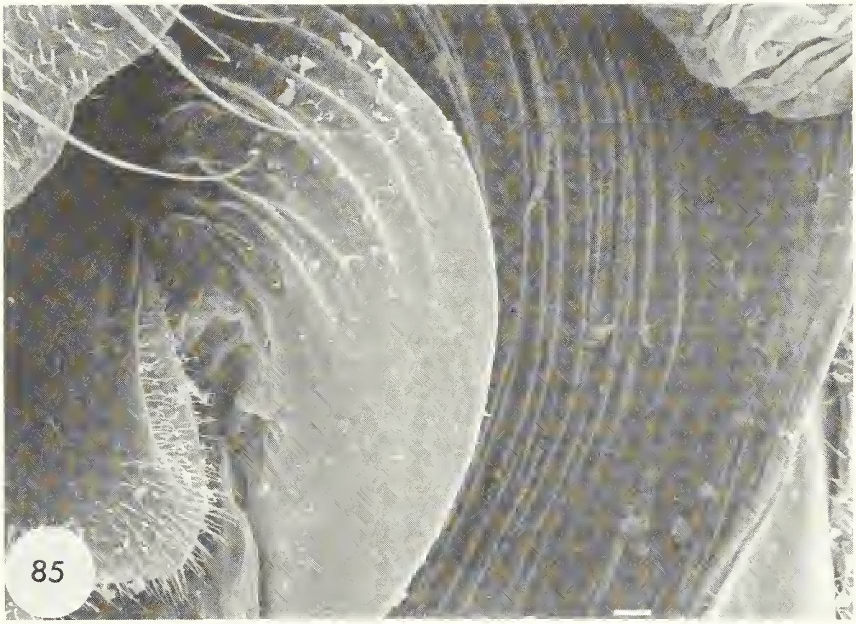
Two male Paratypes and one female Paratype will be presented to the South African Museum.

The two of the Paratype females not in the Albany Museum collection were sent to Dr A. Neboiss, Museum of Victoria, Melbourne, Australia, for examination of their tentorial systems. He later wrote (20.i.91) that the tentorium of *demoori* females looks very much like that in the Australian genus *Caloca* (Calocidae), although there are also differences.

Other material: Southern Cape Province: Jubilee Creek (Station Jub. 1.), tributary of the Homtini River, 33°53'20"S 22°58'15"E (SCR 2A and 3C: FCdM and HMB, 7.iii.1989, 17 putative pupae and 15 empty putative cases; SCR 3B: FCdM and HMB, 7.iii.1989, putative larvae); Jubilee Creek (station at picnic spot) (FCdM and HMB, 7.iii.1989, 1 dead putative pupa and 1 empty putative pupal case).

Note: several *Petrothrincus* larvae (MISC 310c) were collected by NK from the Blaauwkrantz (Bloukrans) River, below Staircase Falls [3323 DC], southern Cape. These larvae, however, differ in colour from those of *demoori,* being plain pale brownish, with a few small, vague muscle spots, very hard to distinguish, on the head, none on pronotum (plain brownish) and a few on mesonotum.





Figs. 84-85. PETROTHRINCIDAE: *Petrothrincus demoori* sp. nov., female.
Material used: SCR 4H (subsequently lost).
84. Female genitalia, scale line 10µm. Note lateral ridges on setose membrane, indicating partial sclerotization, and folds on vulvar scales. 85. Same, scale line 10µm. Note ridges on supragenital plate, also pleural folds.

It is unclear whether these represent a colour variation or another species. The former could well be the case as there is a brown colour variation in some of the *triangularis* specimens from the Langrivier (Jonkershoek) material, the larval cases and abdominal gills are similar to those of *circularis* and *demoori* but not of *triangularis.* Male imagos are needed for clarification.

BIOLOGY of the genus *Petrothrincus.*

The larvae of all three species are found only in clean, undisturbed streams. Larvae of *circularis* and *triangularis* live in stony runs in high, cold, acid mountain streams. *P. triangularis* appears to be restricted to the higher streams, particularly over 3 000ft [= 914 m] altitude, but *circularis* is also found further down, as far as the upper foothills [300-1 000 ft = 91-304 m]. Excellent detailed accounts of the Great Berg River and its tributaries (geology, water chemistry, collecting stations, with details, vegetation and aquatic fauna) can be found in Harrison and Elsworth (1958) and Harrison (1958 a and b). The southern Cape streams are being progressively disturbed by the planting of exotics, timber extraction and bridge building.

P. demoori occurs in places at comparatively low altitudes. De Moor (pers.comm.) noted that *demoori* appears to be restricted to small tributaries as it was not found in the main streams.

Petrothrincus larvae are algal grazers, also ingesting detritus and concomitant animalcules. They are present throughout the year. Adults of *P. circularis* have been collected in February, March and April, of *P. triangularis* in March and May, and of *P. demoori* in March. Oviposition has not been observed. Barnard captured several *circularis* females with an egg mass, a round ball covered with the long hairs from the underside of the female hind wings, still attached to the tip of the abdomen.

Barnard (1934) observed the duration of the pupal stage in *circularis* and *triangularis* finding that it lasted from three to four weeks in February and March.

KEY to the species of the genus *Petrothrincus*

Male Imagos

1. Preanal appendages strongly angulate, claspers wider basally than apically, internal branch of clasper with basal lobe, uncinate spine simple; ninth sternum blunt-ended, slightly indented apically (Figs 38-42). .... *P. circularis*

- Preanal appendages not angulate, claspers evenly wide, internal branch of clasper lacking basal lobe, uncinate spine not simple; ninth sternum bifid (Figs 64-66, 71). 2

2. Preanal appendages with basal lobe, without setulae; claspers narrow; uncinate spine with coiled base; ninth sternum narrow with narrow branches of variable length; aedeagus short, blunt (Figs 74-76). ..... *P. triangularis*

- Preanal appendages without basal lobe, with setulae; claspers broadly quadrangular; uncinate spine without coiled base but with setate basal process; ninth sternum with winged lobes; aedeagus very long, apically narrow in lateral view, broad in dorsal view, with membranous upper part. .... *P. demoori*

Larvae and their cases

1. Cases subcircular, with wide lateral flanges, larvae with pattern of small spots on head; abdominal gills branched. (Figs 47, 48, 61, 81.). 2

- Cases narrowly triangular, lacking wide lateral flanges; larvae with spots on head confluent; abdominal gills simple (on ventral side only) (Figs 69, 70). ...... *P. triangularis*

2. Pattern of spots on head usually forming paired rows on each side of head; spots on pronotum and mesonotum tending to be confluent (Figs 48, 50, 62, 63). .... *P. circularis*

- Pattern of spots on head only partly paired, usually forming larger spots in a single row; pattern of small separate spots on pronotum and a few on mesonotum (Figs 79, 80). ... putative larva of *P. demoori*

Note: in identifying the imagos it is usually necessary to clear the genitalia in KOH, and to study them under a research microscope with a magnification x 100, for some details x 400. The genitalia are very small. For the larvae a stereo microscope with a good magnification is adequate but it is necessary to prop up the larvae on a sand bed to see the top of the head unless the head is taken off. The figures should be used in conjunction with the keys.

Family Barbarochthonidae Scott 1985

Barbarochthonidae Scott 1985: 331, 332 (fig. v), 338; Scott 1986: 231, 234 (table 1), 236.

Type-genus *Barbarochthon* Barnard 1934: 319, 320

The family Barbarochthonidae was erected to accomodate the single genus *Barbarochthon* Barnard. Only one species *B. brunneum* Barnard, is known. It is common in mountain streams in the western Cape Province, is also present, sometimes commonly, in the southern Cape, and has been recorded from Natal.

Recognition

Imago small, mid to dark brown. Vertex with paired interantennary warts and a large posterolateral pair. Male with 3-segmented maxillary palps carried up over face. Pronotum apparently with a single long wart; mesonotum without paired warts but with a median patch of setae which may be present or absent; scutellum suboval with scattered setae. The most useful identification mark is the conspicuous cream-coloured pronotum without visible separate warts.

FAMILY DIAGNOSIS

Imagos

Ocelli absent; eyes large, glabrous; vertex with pair of small interantennary warts and a pair of large posterolateral warts. Antennae about as long as fore wings in male, shorter in female; scape stout, as long as head; flagellum tapered. Maxillary palps in male 3-segmented, little longer than labial palps, usually carried upturned over face, terminal segment not annulate either in maxillary or labial palps. Maxillary palps in female 5-segmented, longer than labial palps.

Pronotum with a pair of long warts fused medially, appearing single; mesonotum without warts but with small median field of setae and a pair of very small anterior setate spots (all are invisible unless the long setae are still present, those are very easily lost, and in any case seem to vary between specimens, being present or absent or partially present); scutellum suboval, sparsely covered with setae. Middle legs with 6 pairs of colourless spines on first to fourth segments of tarsus. Hind legs with 6 pairs on basitarsus, 2 at end of each segment from second to fourth. Fore wings similar in male and female, discoidal cell closed, median cell open; thyridial cell present; anastomosis very clear, forks 1, 2, 3 present. Hind wings considerably smaller than fore wings, male differing considerably from female; in both sexes, discoidal and median cells absent and the venation much reduced, particularly in the male; in male Sc and R_1 fused, stems of fork 1 and of M and Cu_2 barely indicated, sometimes M completely absent, fork 1 and sometimes 2 present; a patch of androconia between bases of RS and Cu_1, covered with long setae; in female Sc and R_1 largely separate, forks 1 and 2 present, stalked; base of M absent. Wing coupling by macrotrichia, and in male in addition by thickly placed marginal setae.

Male genitalia with short two-branched pre-anal appendages; tenth segment bifid; claspers strong, unbranched, with basal lobes; aedeagus stout, divided apically into a dorsal bifid lobe and a ventral lobe with apex scoop-shaped.

Female genitalia with short overhanging paired lobes of tenth tergite. Sternites of tenth segment unsclerotized, without appendages.

Larva

Case dweller; larva rounded; head and pronotum strongly sclerotized; prosternal horn absent. Head dorsally flattened; frontoclypeal apotome with single pair of indentations; antennae very small, at base of mandibles; eyes medium-sized; mandibles large, strongly sclerotized, other mouthparts small, very hairy; ventral apotome rhomboidal, completely separating genae. Mesonotum less strongly sclerotized than pronotum, particularly posteriorly; metanotum membranous with anterior transverse band of setae. Fore leg stout, middle and hind legs long, with very long claws. Abdomen smooth, lacking lateral fringes and lateral tubercles; first abdominal segment with small dorsal hump, lateral humps each with small setate sclerite, ventrally a tough "lip"; gills absent; ninth segment without dorsal plate. Anal prolegs short, with bases fused, strong sclerites present. Anal claw with a long comb of teeth.

Larval case

A long, sometimes very long, tapered tube of dark coloured silk, ornamented with very small sand grains; terminal membrane with circular aperture.

Male pupa

Antennae slightly longer than pupa; labrum transversely ovate; mandibles slender, falcate, inner margin faintly serrulate; maxillary palps 3-jointed, with the labial palps reaching just beyond end of metathorax. Middle tarsi fringed; lateral fringes feebly present from end of sixth segment to eighth, with small tufted ends; wing sheaths reach to ninth segment. First abdominal segment without lappets; second to sixth segments with presegmental dorsal plates, fifth segment with postsegmental dorsal plate, all dorsal plates small. Apical appendages slender, straight, rod-like. Genitalia obscured by brown, somewhat sclerotized integument of ninth segment.

Female pupa

Similar to male but somewhat larger.

Pupal case

Unaltered or shortened larval case closed anteriorly by a membrane with a central boss and transverse slit and having a membrane with a dorsal slit just beyond the pupa; anchored by one or two anterior holdfasts.

Genus *Barbarochthon* Barnard 1934

Barabarochthon Barnard 1934: 319, 321, figs 1a and 15 a-p.

Type species: *B. brunneum* Barnard 1934 (the only species).

Etymology: Generic name neuter, referring to the early Dutch name for the range of mountains where these caddis were discovered. These mountains were termed the "Holland" or Home of the Hottentots (Barbarians).

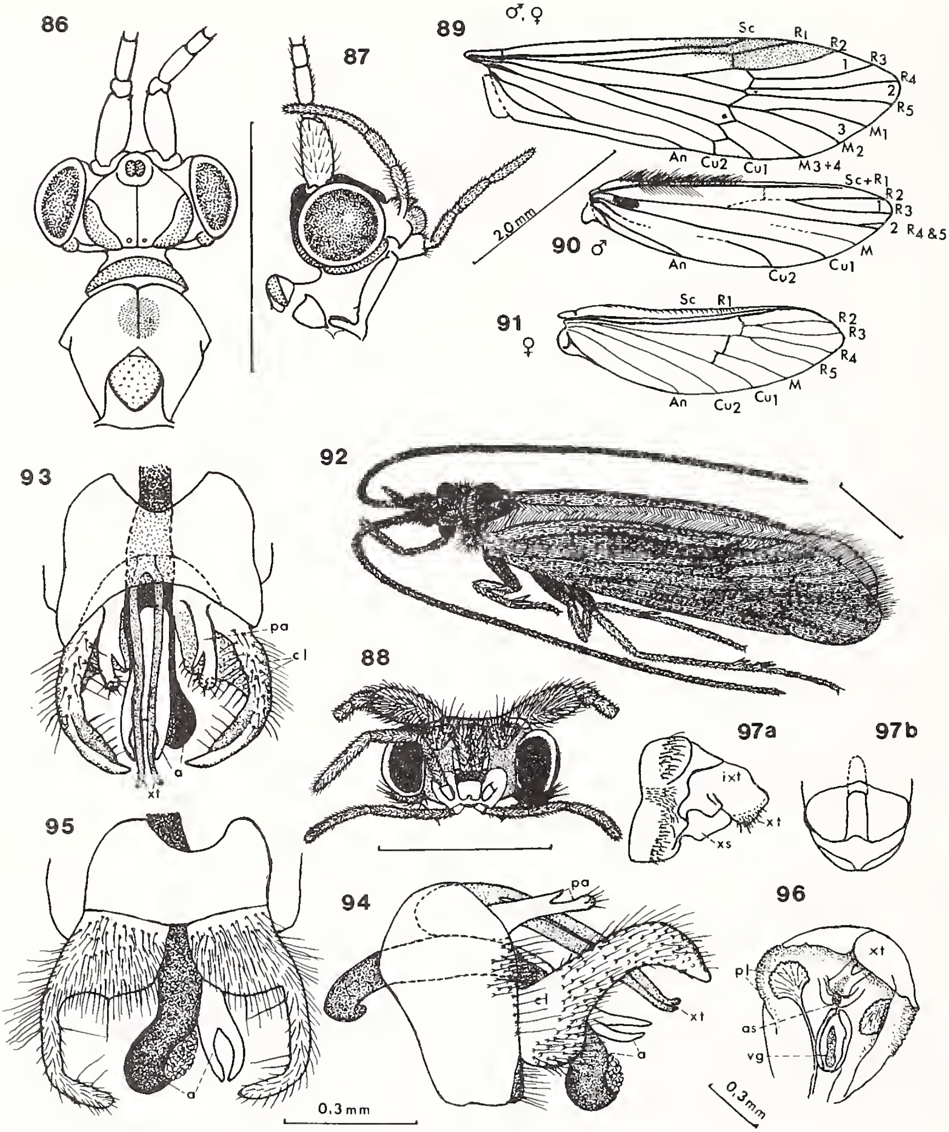
As *Barbarochthon* is a monotypic genus a generic diagnosis is omitted. It is covered by the full description of the species.

***Barbarochthon brunneum* Barnard**
(Figs 86 - 124)

Barbarochthon brunneum Barnard 1934: 319, 321, figs 1a and 15 a-p (male, female, larval and pupal parts, pupal case); Barnard 1940: 643; Harrison and Elsworth 1958: tables 16, 24, 25, 26 (as Sericostomatidae), 207; Harrison 1958a: 260 (as Sericostomatidae); Scott 1985: 338; Scott 1986: 234, 236.

Lectotype male here selected and designated from Barnard's syntypes, South African Museum, Cape Town.

Type locality: western Cape Province, Hottentots Holland Mountains, East side, 4 000ft, [= 1 218 m].



Figs. 86-97. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, male, female
(Scale lines = 1 mm unless otherwise indicated).
Material used: KHB
86. Male: head and thoracic nota, dorsal. 87. Male: head and palps, lateral view. 88. Male: face. 89. Male (and female) forewing. 90. Male hind wing. 91. Female hind wing. 92. Male: entire insect, lateral view. 93, 94, 95. Male genitalia, dorsal, lateral and ventral, showing branches of 10th tergite, pre-anal appendages, claspers and aedeagus. 96. Female genitalia, caudal view. 97a and b. Female genitalia (from Barnard 1934, figs 15g and h, p. 322), a. lateral, b. ventral. (a - aedeagus, cl - clasper, ixs - ninth sternite, ixt - ninth tergum, pa - preanal appendage, pl - pleura, v - vulva, vg - vagina, xt - tenth tergum)

Barnard did not as rule select types, the specimens in his collection being unmarked apart from name, locality, collector(s) and date. The best male from those specimens listed in his 1934 paper and still remaining in the South African Museum collection has been selected as the Lectotype. The other specimens of the same locality and date are regarded as Paralectotype males and females. The 1916 male has not been designated a Paralectotype as it was glued to its mount in small bits. The extant material and the original records are listed after the descriptions of the various stages.

DESCRIPTION OF IMAGOS (Figs 86-99)

Male imago (Figs 86-90, 92-95)

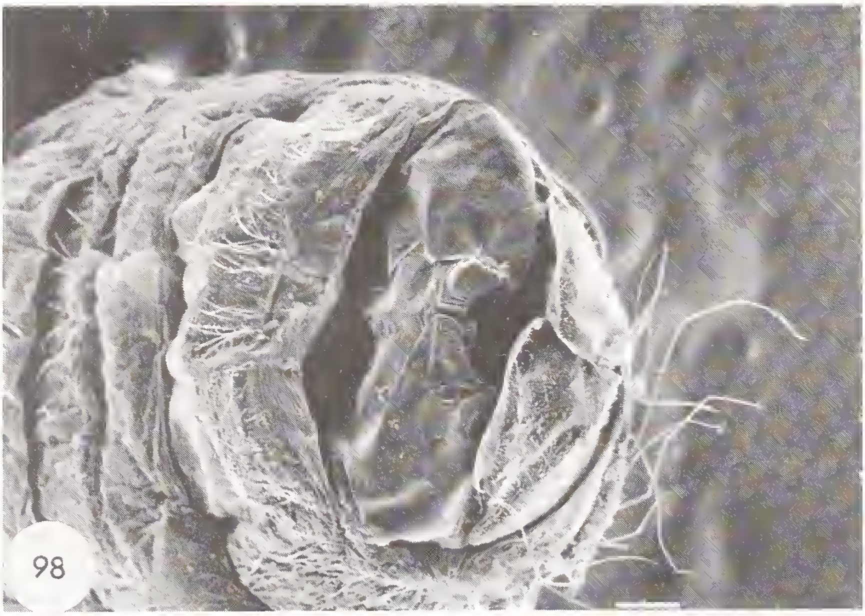
Fore wings 5-6 mm in length.

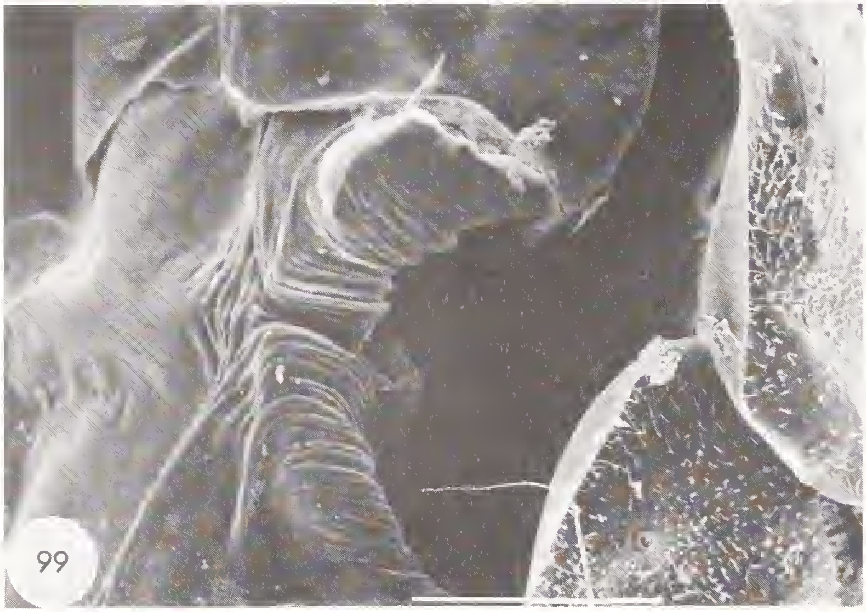
Colour description given by Barnard (1934) as follows: "Head and thorax dark sepia-brown with paler hairs. Legs and antennae fuscous. Wings brown with pale hairs. Membrane with a clear patch on upper margin of thyridial cell and the cross-vein between R_5 and M, and a spot on the connecting vein [= cross-vein] between Cu_1 and Cu_2...". Barnard (1940) added to this a note that fresh specimens, particularly from the Hottentots Holland Mountains, had a pale or white band along the side of the abdomen.

Ocelli absent; eyes large, black, glabrous; vertex with small, paired, contiguous, inter-antennary warts and with posterolateral warts somewhat crescent-shaped; median sulcus present with a small tubercle posteriorly on each side; face with one pair large setose median warts and one pair small lateral warts at antennal bases, these pairs are separated by paired glassy yellow strips. Maxillary palps longer than labial palps; first and second segments together about as long as third, moderately stout, thickly covered with setae. Labial palps 3-segmented; second and third segments subequal, together slightly longer than first. Third segment not annulate in maxillary or labial palps.

Pronotum with a single long wart, evidently representing a fused pair; mesonotum with a median patch of setae and a pair of very small anterior patches, variable in size and presence or absence, practically impossible to see unless the long setae covering them are still present (they are, however, very easily lost and in any case seem to vary between specimens, being present, partially present or absent, as is the case with the Australian family Antipodoeciidae); scutellum with scattered long setae, also difficult to make out unless the setae are still present. Fore wings (Fig. 89) with discoidal cell closed, median open, thyridial present, anastomosis very clear; forks 1, 2, 3 present; R_1 separated from Sc; M_{3+4} fused; Cu_1 present, simple; Cu_2 connected to Cu_1 by a cross-vein; A_2 joining A_1 near base, meeting margin basal to Cu_2 at arculus. Hind wings (Fig. 90) with venation considerably reduced, variable; R_1 probably fused with Sc (compare with female in which they are separate, Fig. 91), ending before margin and bearing a row of macrotrichia near base; RS complete, continuing as R_{4+5}; usually only fork 1 present;R_2 and R_3 present, but only tenuously connected with RS; occasionally R_4 and R_5, which are normally fused, may be separated apically to form a very small fork 2; M undivided, may be completely absent but, if present, most of its stem is missing or very faint, as are the stems of fork 1 and Cu_2; Cu_1 complete, simple; anals short; a cluster of scent scales (androconia) always present between bases of RS and Cu_1, covered by a dense tuft of setae. Only one cross-vein, sometimes very faint, between Sc + R_1 and faint base of fork 1. Wing-coupling by many strong setae along basal half of hind wings, also by the macrotrichia on SC + R_1. Jugal lobes large.

Genitalia (Figs 93-95) with short two-branched preanal appendages, the inner branch pointed, the outer with expanded setose tip; tenth segment bifid, forming 2 long slender processes; strong single-jointed claspers each with broad inturned basal lobe (Fig. 95); aedeagus divided towards





Figs. 98, 99. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, female
(Scale lines = 1 mm unless otherwise indicated).
Material used: KHB
98. Female genitalia, caudal view. Scale line 100 µm. Note 10th tergites on right, and very simple genitalia.
99. Female genitalia, same. Note tergites and apparent curling in of pleura-like folds, into vulva.

middle into dorsal apically bifid lobe and ventral lobe with scoop-shaped apex and membranous in-fill.

Female imago (Figs 91, 96, 97, 98, 99)

Female larger than male; fore wings 6.5-7.0 mm in length.

Vertex with setose warts differing slightly from those of the male in position and shape, the interantennary warts being slightly separate and the posterolateral warts being subovate. Antennae shorter and more slender than in male. Maxillary palps 5-segmented, longer than labial palps; both palps smaller than in male.

Fore wing venation as in male; hind wings (Fig. 91) with forks 1 and 2; R_1 largely separated from Sc and, as in male, connected to stem of fork 1 by a cross-vein; RS present, complete; apex of M present, simple, lacking basal part of stem; stem ends just beyond cross-vein; Cu_1, Cu_2 and A all present, entire. Wing coupling by macrotrichia. Jugal lobes large.

Genitalia with short overhanging paired lobes of tenth tergites; ninth sternites evidently soft, unsclerotized, not rugose as in Hydrosalpingidae. Genitalia much simpler than in Petrothrincidae. Position of vagina shown in Fig. 96. There are no appendages.

Figs 98, 99 show finely rugose pleura-like folds, evidently within the vulva. In another female the vulvar opening appears to be plugged.

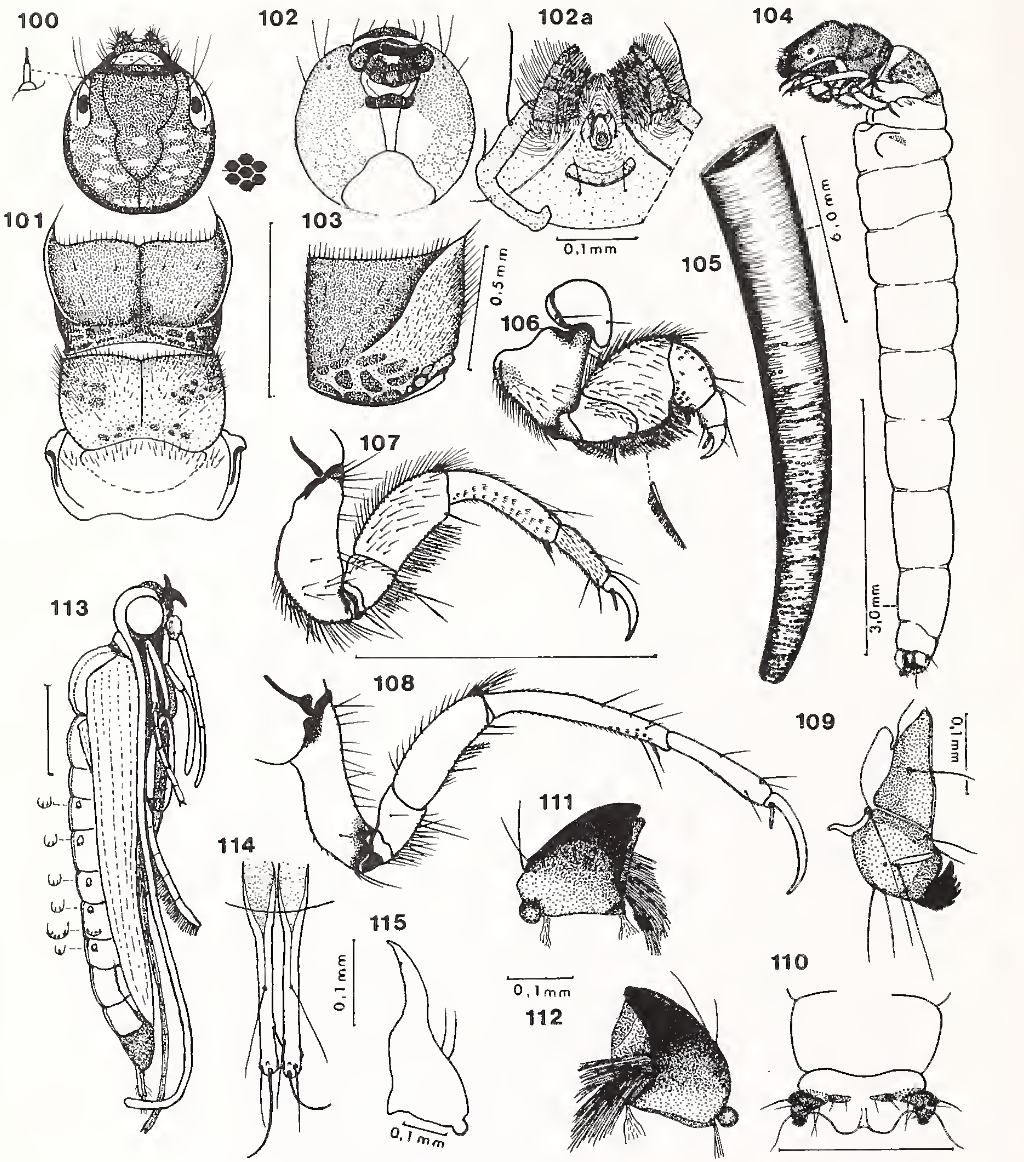
DESCRIPTION OF MATURE LARVA (Figs 100-112; 116-124).

Description from material from the Homtini River, southern Cape, from stones in current (SCR 5A: FCdM and HMB, 8.iii.89; MISC 251a: KMFS and BCW, 27.v.70) compared with Barnard's specimens and drawings.

Length of larva up to 8 mm; larva rounded.

Head dorsally flattened (used to plug case), strongly sclerotized, blackish-brown to rich chestnut in colour, with pigment arranged in an apparent honeycomb pattern (see Figs 100, 102 and 119-121); ventral apotome narrowly quadrangular (Fig. 102), completely separating genae in young larvae, difficult to distinguish posteriorly in older larvae in which only the dark brown anterior bar may be clearly visible. Eyes fairly small, under small clear lenses in white area. Antennae very small (Figs 119-121), on side of head near base of mandibles. Labrum (Fig. 102) small, rounded, partially retractile. Maxillae and labium very tightly packed into a small space behind mandibles; maxillary palps clear, thick, very hairy; stipes and cardo fused forming a single stout structure; labium and labial palps stout, both sets of palps on large bases; a dense brush of setae anterior to labium. Mandibles (Figs 111, 112) very heavy, blackened apically due to strong sclerotization; left mandible with two inner brushes of setae set deep in a hollow; right mandible with a single brush; brushes apparently variable, in some instances right one appears to be missing; both mandibles appear to have a cutting edge and two very long, strong basal ligaments (shown cut short in Figs 111 and 112); setae very strong but not feathered; apex long with three or four teeth when unworn (as in the Petrothrincidae the mandibles may show heavy wear as in Figs 111, 112).

Pronotum strongly sclerotized with carina ending in strong anterolateral points, with strongly marked dark sepia pattern behind carina (obvious on the pale greenish-yellow background), and with small posterolateral divisions seen in lateral view (Fig. 103). Mesonotum with sepia muscle spots on greenish-orange background, less strongly sclerotized particularly on posterior half. Metanotum membranous with anterior band of setae, in colour pale greenish mixed with orange, with small sclerites



Figs. 100-115. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larva and case, pupa (Scale lines = 1 mm unless otherwise indicated).
100, 101. Mature larva, head and thorax, dorsal. 102. Younger larva, head, ventral. 102a. Same. Maxillary and labial palps. 103. Pronotum, lateral. 104. Mature larva, habitus, lateral. 105. Larval case. 106. Fore leg and pre-episternum. 107, 108. Middle and hind legs. 109. Anal proleg and claw, lateral view. 110. Anal prolegs, dorsal view. 111,112. Right and left mandibles, ventral view. 113. Male pupa, habitus. 114. Same, anal appendages further enlarged. 115. Pupal mandible.

as shown in Barnard's drawing of metanotum (Barnard 1934 Fig. 15i) not visible. Pre- episternum large with apex bluntly rounded (Fig. 106). Pleural sclerites with black marks. Legs (Figs 106-108) whitish to pale brown in life with light brown to sepia markings. Fore leg stout; coxa large; trochanter 2 and femur with setal brush along ventral margin but without distoventral process; ventral brush with plumose setae and a few peg-like ones; tibia with small clusters of minute setulae and two blade-like setae on disto-ventral angle, one larger than the other; claw stout, same length as tarsus. Middle leg longer, more slender; trochanter 2 and femur with partly plumose setal fringe; tibia with many minute clusters of setulae; tarsus set with small setae; claw same length as tarsus. Hind leg much longer; coxa slender, curved; femur with a few plumose setae; tibia with a few setulae; tarsus without small setae; claw nearly as long as tarsus. All three claws stout with sharp apex and stout seta near base.

Abdomen (Figs 104, 109, 110 and 122-124) orange-coloured anteriorly, fading and mixing with pale green posteriorly in life, white or cream in spirit; first segment with low dorsal hump, with lateral humps each with small pubescent sclerite, and with ventrally an apparent toughened area or "lip"; ninth segment without dorsal sclerite; anal prolegs short; anal claw very small, with dorsal comb; tenth segment with two small dorsal sclerites of variable length (between anal prolegs), with large, dark, lateral sclerites and ventral sole plates, lacking tufts of setae (Figs 109, 110). Anal claw as seen in the SEM micrographs (Figs 122-124) shows a few teeth of comb just above anal claw, continued round to back as a number of sharp teeth, about 8-10 in all.

Larval case (Fig. 105)

A long, often very long, slender, curved, tapering, dark- coloured, silken tube, ornamented particularly towards the posterior end with rows of minute sand grains; terminal membrane with circular aperture.

The tube looks more brightly coloured when it contains a live larva as the orange-green colouring of the abdomen and parts of the thorax show through.

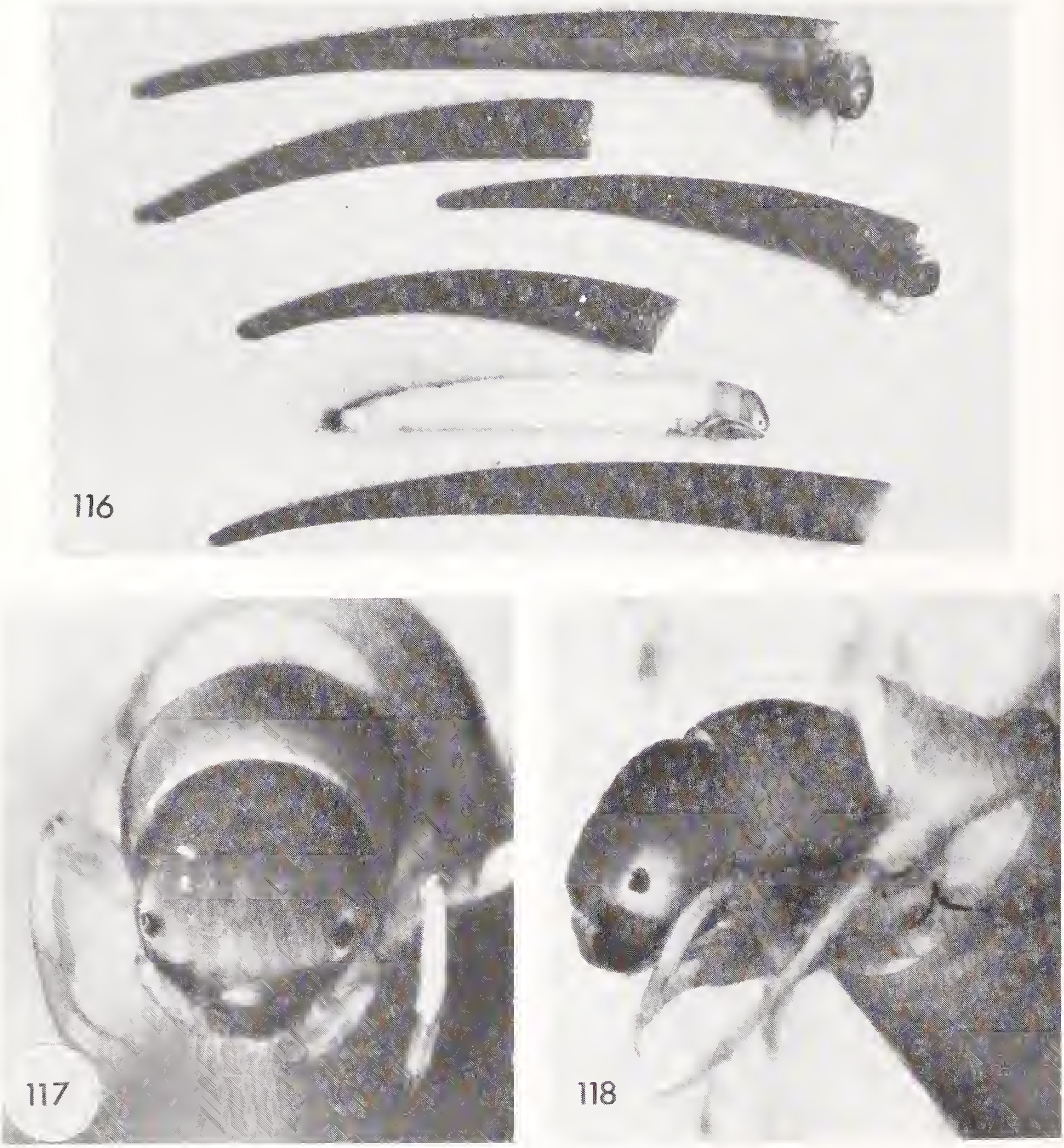
DESCRIPTION OF PUPA (Figs 113-115).

Male pupa

Antennae slightly longer than body. Labrum transversely ovate. Maxillary and labial palps extend to first abdominal segment. Mandibles slender, falcate, inner margin very slightly serrated. Middle tarsi fringed. Lateral fringe present from sixth segment, ending in a tuft on eighth segment. Gills absent. Fore wing sheaths reaching to beginning of ninth segment. Presegmental dorsal plates on second to sixth segments (2 teeth each); postsegmental dorsal plates on fifth segment (4 teeth); ninth segment apparently lightly scelerotized, brown in colour. Anal appendages slender, rod-like, each with a long stout apical seta, and two or three long slender ones.

Pupal case

At pupation the long posterior end of the larval case is usually cut off and the terminal membrane replaced by a new one with an oval vertical slit; the anterior end is closed by a convex membrane with narrow horizontal slit. Should the end of the larval case not be cut off at pupation, the terminal membrane of the larval case remains and the pupal membrane is formed within the case below the end of the pupa. The pupal case is anchored underneath a stone or on vegetation by one or two anterior holdfasts.



Figs 116-118. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larvae.
Material used: MISC 270c.
116. Photograph of two larvae in cases, one larva ex. case, and three empty cases. 117. Larva showing dorsal view of head. 118. Lateral view of head and thorax of larva in case. Photographs by J.C. Hodges, Jr.

DISTRIBUTION

South Africa: the western and southern Cape Province, in mountain streams in the coastal ranges; and Natal where it has been recorded from Karkloof, near Howick.

MATERIAL EXAMINED

South African Museum material

Pinned material

Lectotype: Southwestern Cape: Hottentots Holland Mountains [3418 BB], 3 500-4 000 ft [= 1 066-1 218 m] (KHB and HGW, i.1933, male).

Paralectotypes: Southwestern Cape: Hottentots Holland Mountains [3418 BB], 3 500-4 000 ft [= 1 066-1 218 m] (KHB and HGW, i.1933, 8 males).

Other material: Southwestern Cape: Hottentots Holland Mountains [3418 BB], 3 500-4 000 ft [= 1 066-1 218 m] (KHB, i.1916, male, glued to its mount in small bits).

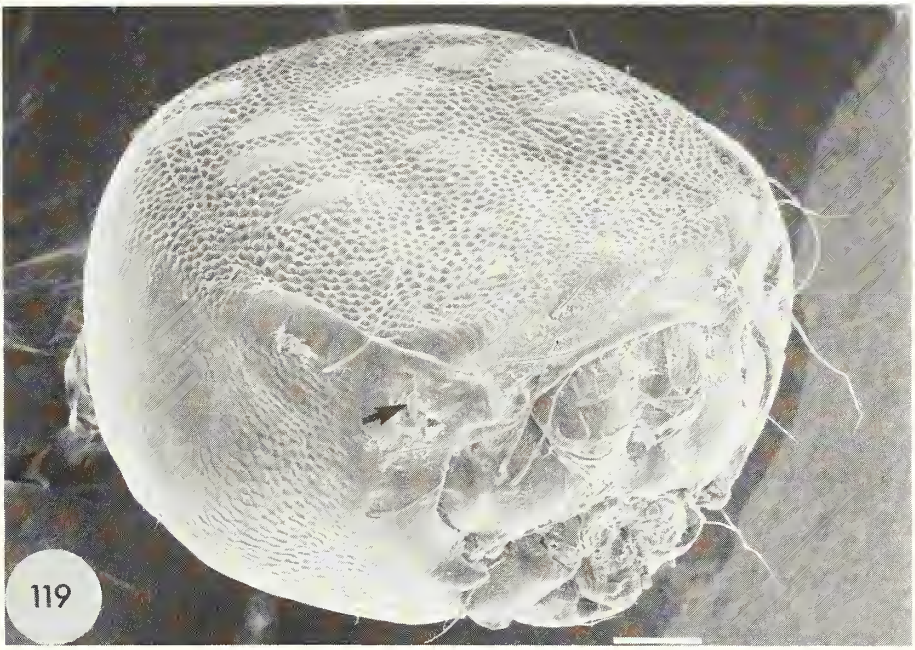
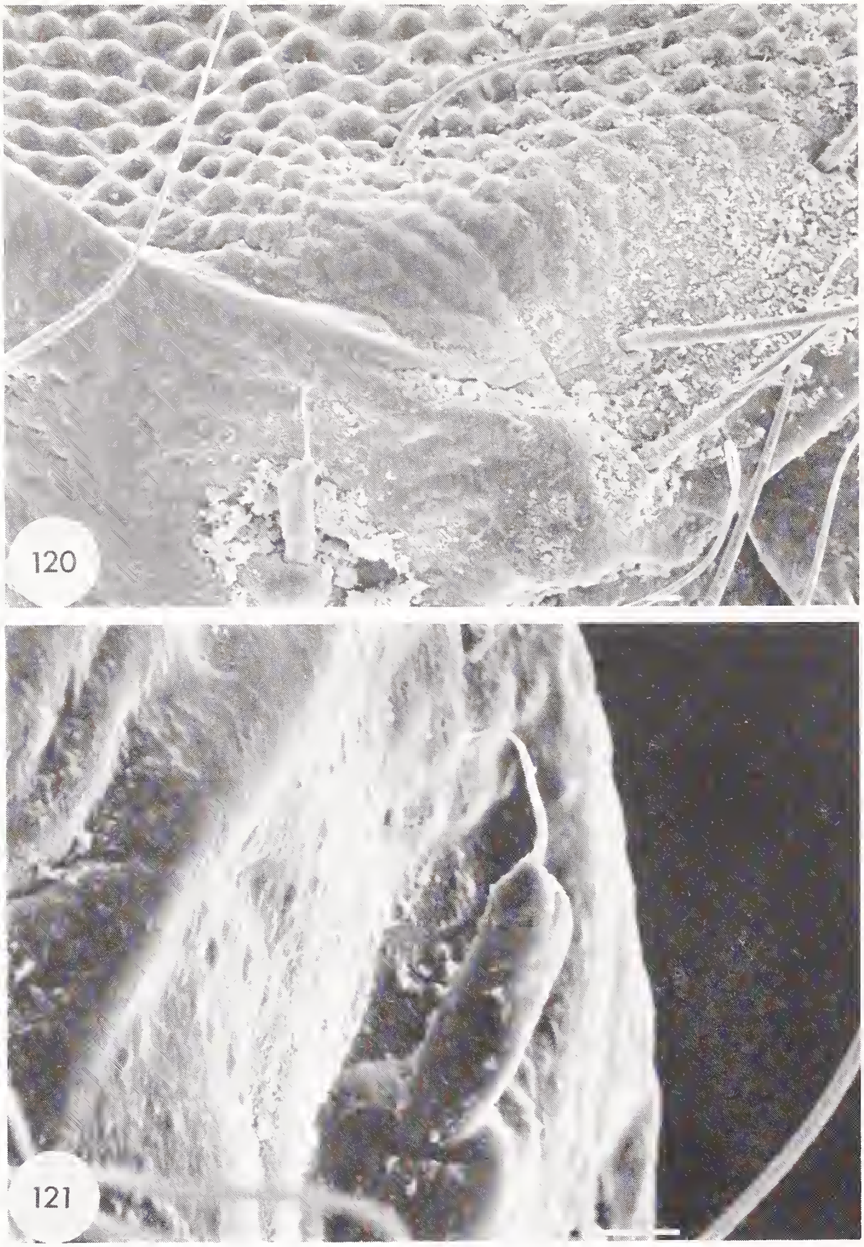


Fig. 119. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larva.
Material used: MISC 251a.
Scale line 100 μm. 119. Head of larva, to show sculpturing of cuticle, tightly packed mouthparts, and position of very small antenna (indicated by arrow).



Figs. 120, 121. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larva.
Material used: MISC 251a.
120. Scale line 10 µm. Part of head of larva showing antenna. 121. Scale line 10 µm, Antenna.

Material in spirit

Paralectotypes: Southwestern Cape: Hottentots Holland Mountains, East side, 3 500-4 000 ft, [= 1 066-1 218 m] [3418 BB] (KHB and HGW, i.1933, 21 males, 12 females).

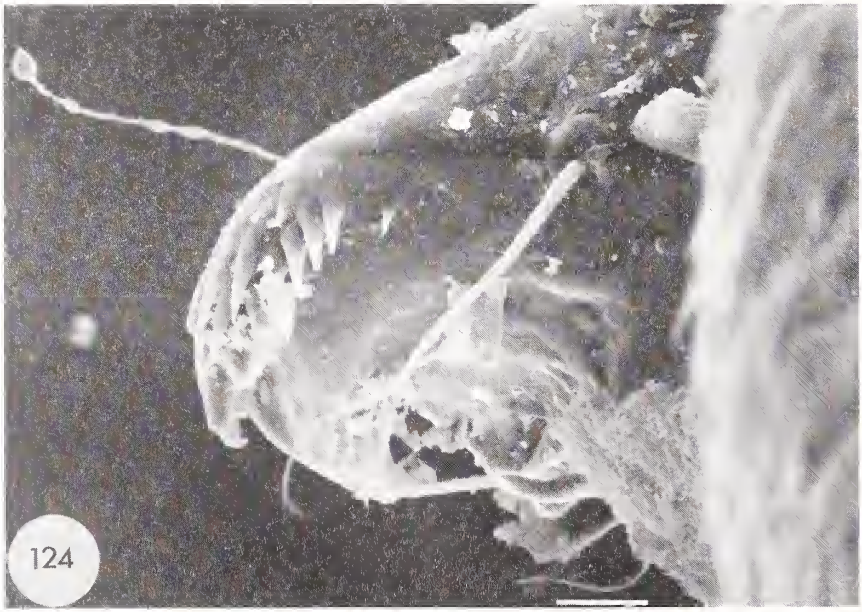
Other material: Southwestern Cape: Hottentots Holland Mountains, East side, 3 500-4 000 ft, [= 1 066-1 218 m] [3418 BB] (KHB and HGW, i.1933, larvae and few pupae); Wellington Mountains [3318 DB], 3 000 ft, Witte River, Bains Kloof (KHB, ix.1922, 2 males); Cape Peninsula, Table Mountain, Orange Kloof [3318 CD] (KHB, 1.iii.1933, pupal cases, largely empty but with a few pupae). [From the Table Mountain material Barnard (1940) obviously had had imagos, since lost, which he used in establishing its identity.]

Albany Museum material

Material in spirit

Western Cape: Great Berg River, Driefontein [3319 CC], (MISC 89: KMFS, 12.xii.54, 1 male with pupal pelt and case); same (GBG 142B: ADH, 22.xi.50, 1 pupa); Great Berg River, Railway Bridge [3319 CC] (GBG 780, 783: KMFS, x.53, 1 male, 1 female); Great Berg River, Sneeugat [3319 CC] (Source; GBG 372A(1): ADH, 28.ix.51, larvae); Great Berg River, Driefontein, (MISC 139: KMFS, 8.x.59, larvae); Great Berg River, Assegaibos [3319 CC] (MISC 288d: KMFS, 30.i.76, 2 larvae); Smalblaar River, tributary of the Breede River, Du Toit's Kloof [3319 CA] (MISC 217: RD,

Fig. 122. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larva.
Material used: MISC 251a.
Scale line 100 μm. Posterior segments of larval abdomen showing anal claws (ex. MISC 251a).



Figs. 123, 124. BARBAROCHTHONIDAE: *Barbarochthon brunneum* Barnard, larva.
Material used: MISC 251a.
123. Larva: Right anal claw seen from outer side, showing long claw with smaller hook and smaller teeth curling round to the inner side. Scale line 100 μm, 124. Left anal claw seen from inner side, showing row of teeth curling right round to the inside, making in all a comb with about 8-10 teeth. Scale line 100 μm.

i.1962, 1 larva); Upper Witte, Happy Valley [3319 CA], (MISC 269d: KMFS, 3.x.74, 1 larva); Upper Witte, Happy Valley (MISC 304e: KMFS, 6.ii.76, 2 larvae, 1 pupa); Upper Witte, Happy Valley, higher up, (MISC 270c: KMFS, 3.x.74, 8 larvae); Witte River, Wolwekloof (MISC 291c: KMFS, 30.xi.76, 2 larvae); Witte River, main stream [3319 CA] (MISC 296b: KMFS, 2.ii.76, 23 larvae); Witte River, Leeuklip Kloof tributary [3319 CA] (MISC 267a: KMFS, 3.x.74, 4 larvae); Palmiet River near Elgin [3319 AA] (MISC 48: ADH, 17.xii.52, 1 male); Table Mountain, Disa Gorge, Orange Kloof [3318 CD] (MISC 285g: KMFS and BCW, 27.xi.76, 4 larvae) and (MISC 286d: KMFS and BCW, 27.i.76, 1 prepupa in case); Langrivier, tributary of Eersterivier [3318 DD], Jonkershoek Nature Reserve, Stellenbosch (JMK, different times of the year, larvae); Upper Langrivier (MISC 271b: KMFS, 4.x.74, 2 larvae).

Southwestern Cape: Vetrivier, Garcia's Pass, above Riversdale, tributary near top of pass, below Tolhuis [3421 AA] (MISC 306L: KMFS, 9.ii.76, 1 larva).

Southern Cape: Homtini River, Homtini Pass at road bridge [3322 DD] (MISC 251a: KMFS and FMC, 27.vii.70, 102 larvae); Homtini River, Phantom Pass [3322 DD] (MISC 278e: KMFS, 22.i.76, 10 larvae); Karatara River Jubilee Creek tributary (SCR 2A and 3C and SCR 3B, 6 and 7: FCdM and HMB, 7.iii.1989, putative pupae and larvae); Blaauwkrantz River, Tsitsikama, [3323 DC], 180 m (SU 67: HB, 25.i.59, 4 larvae); Kruis River, [3319 AB] (FRW 164H, 166J, 174D, 183F: ADH and JDA, 8.iii.60, all larvae); Storms River [3423 BB] (FRW 159Z, 186C, 8.iii.60, ADH and JDA, larvae); Kaaiman's River [3322 DC] (FRW 180F: ADH and JDA, 10.iii.60, larvae).

MATERIAL CITED IN LITERATURE

Barnard (1934): Hottentots Holland Mts., 3 500-4 000 ft (KHB, January 1916, 1 male and KHB and HGW, January 1933, males, females, larvae and pupae); Wellington Mts, 3 000 ft (KHB, November 1922, 1 male); Table Mt, Cape Peninsula, 1 000 ft (KHB, 1st March 1933, 1 pupa, empty cases); Montagu Pass, north of George, Outeniqua Range (HWG, April 1933, larvae) [appear to have been lost].

Barnard (1940): Upper Olifants River, north of Ceres,(KHB and CWT, October, 1937, males and females) [appear to have been lost].

Jacquemart (1963): Bainskloof [=Bain's Kloof] about 10 miles E.N.E. Wellington [the Witte River] [3319 CA]. In the eastern part of the kloof: fast-running stony mountain stream. 12.2.1951. 1 male.

Additional material

Morse (in litt 16.xii.74), 1 male from Karkloof near Howick, Natal [2930 AC], 27.x.70, H. and M. Townes *leg*.

BIOLOGY of genus *Barbarochthon*

Much background information regarding the localities on the Great Berg River can be found in Harrison and Elsworth (1958), as was indicated for *Petrothrincus*. A brief faunistic summary for the Berg River (for Trichoptera see pp. 260-263) is given in Harrison (1958a). In these studies *Barbarochthon brunneum* is usually referred to by name and placed under Sericostomatidae or sometimes Beraeidae. *Barbarochthon* larvae were commonly found from the uppermost zone of the Berg (sponges and cliff waterfalls, altitude from 4 000-5 000 ft [= 1 219-1 514 m]; cliff waterfalls

down to 2 500 ft [= 762 m]); through the Mountain Torrent Zone at 1 000-4 000 ft, [304-1 219 m]; Assegaaibos main stream in the Franschhoek Forest Reserve - Stn 1 at 1 000 ft [= 304 m]; to the Foothill Stony Run Zone at 300-1 000 ft [= 91-304 m], subdivided into two subzones, an upper one which included stations 3 and 5 at Driefontein and the Groot Drakenstein Railway Bridge respectively and a lower one which included at its upper end Station 9 at Simondium (Harrison and Elsworth, 1958, collecting stations shown in Plates X-XII). From the tables of significant animals from stones-in-current, from *Scirpus,* and from marginal vegetation (Harrison and Elsworth 1958: Tables 16, 24, 25 and 26) it seems that *Barbarochthon* larvae are far more abundant in the marginal vegetation than in either the *Scirpus* or the stones-in-current biotopes. In the marginal vegetation they were notably present in considerably higher percentages of the fauna in summer and autumn in the Mountain Torrent Zone (Stn 1) and in spring, summer and autumn in the upper foothills (Stn 3) but always present in lower numbers at both these stations during other seasons. *Barbarochthon* is present in much smaller numbers and only at certain times of the year at Stations 5 and 9, the lowest stations at which it occurred at all.

Barbarochthon larvae have also been recorded (see material, above), but not usually commonly, from streams in the southern Cape.

The larvae live mainly amongst marginal vegetation and on submerged or partially submerged clumps of *Scirpus digitatus.* They can be found in both fast current and backwaters. They feed on leaves, crawling about actively at all seasons of the year. They are also present, though much less commonly, on stones in current and are evidently capable of feeding there. They do not, however, use leaves in making their cases which are always of silk and are ornamented with sand grains. The structure of the mandibles bears out the method of feeding, the inner margin having a cutting edge and the sturdy brushes of setae presumably being used to help hold the leaves.

Adults have been collected in the Cape Province in October, November, December and January. A single male was collected at Karkloof near Howick in Natal in October.

DISCUSSION

Over the years the author has drawn up comparative tables for adults, larvae and pupae in order to compare the genera *Hydrosalpinx, Petrothrincus* and *Barbarochthon* with a number of families: both those into which earlier authors attempted to place them, and certain of the Australian families which seemed comparable at least to some degree. The tables were derived from the author's notes and drawings for the three South African genera and from the best sources that could be found for the families considered. Literature consulted in building up the tables and in the preparation of the present paper included Cowley (1976 and 1978), Harrison and Elsworth (1958), Harrison (1958a and b, 1965 and 1978), Lepneva (1966 (1971)), Mosely (1939), Mosely and Kimmins (1953), Neboiss (1977, 1981, 1983, 1984, 1986, 1988 and 1991a and b), Ross (1967 and 1978), Scott (1955), Ulmer (1951 and 1955).

Based on the author's analysis of the literature she selected for comparison the Australian families Helicophidae, Calocidae and Antipodoeciidae as possibly being nearest to the three genera *Hydrosalpinx, Petrothrincus* and *Barbarochthon.* To these were added the Bereidae and the Sericostomatidae, primarily because of their repeated linkage with the three in the literature, and the South American family Anomalopsychidae as a Neotropical comparison. It should be mentioned that not all the Australian families had been studied and that a number of other families, for example the Molannidae, Brachycentridae and Thremmatidae, had been included in earlier analyses.

Having placed the three genera in three families, Hydrosalpingidae, Petrothrincidae and

Barbarochthonidae, it is necessary to set the families in their place in the classification of the Trichoptera. All clearly belong to the Sub-Order Integripalpia Martynov (1924) (see Schmid, 1980, pp. 14-17). All have adults with maxillary palps either 3 or 5-segmented in the male, 5-segmented in the female, and with the last segment simple. The fore wings have the discoidal cell closed, rather long, the median cell open and fork 1 sessile. In the male genitalia the ninth tergum is narrowed, the tenth tergum is somewhat hood-like or present but elongated and forked, the phallic apparatus is provided with an aedeagus, and in the Petrothrincidae with paired parameres. In the female the genitalia are without cerci but may have small apical dorsal appendages, evidently modifications of the tenth tergites. There are definitely separate anal and vaginal apertures and, in the Petrothrincidae, a clear supragenital plate and vulvar scales. The larvae are eruciform and live in portable cases in which they are anchored by their short anal prolegs which in the Petrothrincidae are rather longer than is usual though not as long as in the Annulipalpia.

The division of Integripalpia to which all three appear to belong is the Superfamily Leptoceroidea Schmid (1980). The Leptoceroidea were characterized by Flint (1981, quoting Ross, 1967) as having lost their ocelli, the male fore wings retaining M_4 in primitive families, the supratentorium reduced and larval pronotum without a crease. The last appears to suggest a posterior suture of the pronotum as opposed to an anterior suture in the Limnephiloidea. Flint (1981), however, could find no consistent pattern in this, with which the present author agrees. In fact some taxa within one group may have both, others neither. Flint further characterized the leptocerid branch (the Leptoceroidea Schmid) as having larvae which lack a prosternal horn, have bifid tubercles on the eighth abdominal segment only, and lack a strongly sclerotized dorsal sclerite on the ninth abdominal segment. None of the three South African families has a prosternal horn. In the Hydrosalpingidae there are bifid tubercles on the eighth segment only and a weak dorsal sclerite on the ninth segment. Neither of the other two families has either bifid (lateral) tubercles or a dorsal sclerite on the ninth segment. It should be noted that, in southern Africa at least, certain genera of Leptoceridae (for example, *Setodes, Trichosetodes* and *Leptecho*) do have a dorsal sclerite on the ninth abdominal segment, in some cases strongly sclerotized. Judging from the illustration in Wiggins (1977), the North American *Setodes incertus* (Walker) also does. On the other hand, many leptocerids do not, so that it would not seem to be a good distinguishing character for the Leptoceridae, and therefore for the Leptoceroidea.

Weaver (1983, 1984), in his proposed classification of the Trichoptera, splits Schmid's Leptoceroidea into Sericostomatoidea Stephens (1836) and Leptoceroidea, both included in his new Infraorder Brevitentoria. Schmid (1980) indicated this division in his phyletic tree by its branching. In such a split the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae would all fall into the Sericostomatoidea rather than the Leptoceroidea. This is indicated by the apparent relationship of all three to the Australian families Helicophidae, Calocidae and Antipodoeciidae, and possibly of the Hydrosalpingidae and Barbarochthonidae also to the Beraeidae. The characters given by Weaver, however, are so few as to render comparisons difficult. Certainly all three families share with his Sericostomatoidea adults with tibial spurs 2, 2, 4 (in common with many southern hemisphere families and certain others) and lacking ocelli, and larvae which are phytophagous. In the larva the pre-episternum (Weaver's trochantin), however, is not small but large in both Petrothrincidae and Barbarochthonidae and is normal in Hydrosalpingidae, and the tergite on the ninth abdominal segment is present, although weak, in Hydrosalpingidae but is absent from the other two families.

Incidentally, Weaver gives the larvae of his Sericostomatoidea as phytophagous and those of Leptoceroidea as predatory. In fact most southern African Leptoceridae show the whole gamut of feeding habits from purely phytophagous to mainly carnivorous, the latter being rare. The related Calamoceratidae are certainly plant-eaters.

Although the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae were individually compared with the Brachycentridae and the Thremmatidae there seems to be no point in drawing comparisons between them, since the latter families fall into the Limnephiloidea not the Leptoceroidea (*sensu* Schmid). Molannidae falls into the leptocerid branch rather than the sericostomatid branch of the Leptoceroidea and so no detailed comparison between it and the three families is necessary.

In the present paper Dr F. C. de Moor, using cladistic analyses, has compared the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae with the families in Weaver's Sericostomatoidea and with the Antipodoeciidae.

The original decision to treat the three genera *Hydrosalpinx, Petrothrincus* and *Barabarochthon* as each belonging to a new family is supported by the cladistic analyses. The three families do appear to fit into the Sericostomatoidea, as may be seen in both analyses (Figs 125, 126). It appears from the cladogram based on 44 characters (Fig. 126) that the closest relatives of the Hydrosalpingidae are all Australian or South American and those of Barbarochthonidae and Petrothrincidae are the Beraeidae and Antipodoeciidae. These are of course preliminary results, however, it is of interest that this cladogram separates out into two branches, one almost exclusively Australian, the other almost exclusively non-Australian, with the South African families divided between the two.

ZOOGEOGRAPHICAL NOTE

Ross (1967), when discussing the origin of the fauna of Eurasia- Africa-Madagascar, referred to two of these endemic South African genera, *Petrothrincus* and *Hydrosalpinx.* He queried whether they, together with *Paulianodes* (Philopotamidae) and the Pisuliidae, were not survivors of the Cretaceous or more recent immigrants that had become extinct in their original, unknown home, or were not even older lineages arising from ancestors that had reached Africa or Madagascar perhaps as early as the Jurassic.

Petrothrincus, Hydrosalpinx and *Barbarochthon* of the presently defined families Petrothrincidae, Hydrosalpingidae and Barbarochthonidae are all endemic to South Africa and indeed, almost entirely to the Cape Province, where they are found in the acid mountain streams of the western Cape coastal folded belt and in its extension into the southern Cape. In this area there are many relicts of the cool-adapted Gondwanaland fauna to which the present three families most probably belong (see also Scott, 1986). This is borne out by the close linkage (Fig. 126) of the Hydrosalpingidae with the Helicophidae, a family also found in South America and Australia.

In early Jurassic times, over two hundred million years ago, Africa lay well to the South of where it lies now (Harrison, 1978 and W. J. de Klerk, pers. com.), still linked with Antarctica, Australia and South America to the South. What is now our south-west coast would have been much cooler and wetter. It would have formed a southern part of the very large continent, Gondwanaland, of which the northerly parts were becoming subtropical and then tropical as they slowly drifted northwards. Gondwanaland finally broke up in the late Jurassic and the continents eventually reached something like their present positions.

Many cool-adapted caddisflies must have become extinct as the climate warmed up, but quite a number did survive: in addition to the Hydrosalpingidae, the Petrothrincidae and the Barbarochthonidae, certainly also the southern African Sericostomatidae (6 genera), many species of *Athripsodes* (Leptoceridae) and certain genera, for example, *Leptecho* (also Leptoceridae), and the hydropsychid genus *Sciadorus.*

Ross (1967) was therefore correct in tentatively placing *Petrothrincus* and *Hydrosalpinx* as survivors of the Cretaceous rather than as more recent immigrants. They might indeed have an older

lineage, perhaps from the Jurassic or even earlier as was also suggested by Ross. Ross could quite justifiably have included *Barbarochthon* with them. Wiggins (1984) suggested that the origins of the Trichoptera could have been in the early Mesozoic or even the Permian (in the Palaeozoic). Whenever they originated, it must have been prior to the final break-up of the southern continents in order for there to be links between some of the southern families found on the present day continents of South America, South Africa and Australia.

A CLADISTIC ANALYSIS OF CHARACTER STATES IN THE TWELVE FAMILIES HERE CONSIDERED AS BELONGING TO THE SERICOSTOMATOIDEA (by **F. C. de Moor**)

A cladistic analysis of the states of a number of characters of the three recently erected endemic South African families of Scott (1985), the Antipodoeciidae and the 8 families recognised as belonging to the Sericostomatoidea Stephens (1836) *sensu* Weaver (1983) was carried out. For the analysis 59 characters (from the larvae, pupae and adults) each with two to several possible states, were chosen (Table 1). Characters were selected from morphologically useful identification features within these twelve families that appear to belong to the Sericostomatoidea. They were chosen irrespective of whether they were shared by members of the three new South African families or were considered to contribute to a phylogenetic evaluation of the families. Characters considered as plesiomorphic were given a state of 0, and numerical values for the other characters assumed that they were derived. Where the primitive or derived status of characters could not be decided upon enumeration of character states commenced with one. The family Anomalopsychidae was chosen as the outgroup as it was the only family in the Sericostomatoidea with ocelli and showed the highest number of character states considered as being plesiomorphic. The full selection of characters is not included for this preliminary analysis as it is still being refined and will be presented when an analysis of the genera of these families can be conducted.

In a number of instances characters showing several states were found within one family (see Table 1 for definition of characters). For the Sericostomatidae wing venation characters were shared with the three endemic South African families and Antipodoeciidae (forks 1, 2, 3 present in male fore wings), or with the Calocidae, Conoesucidae and Anomalopsychidae (forks 1, 2, 3, 5), or only with the Chathamiidae (forks 1, 2). Likewise for the forks in the male hind wings alternative character states existed in the Sericostomatidae (states 1 or 2), Barbarochthonidae (states 3 or 4), Beraeidae (states 5 or 7), Helicophidae (states 6 or 7), Calocidae (states 1 or 4), Anomalopsychidae (states 1 or 2), Conoesucidae (states 5 or 7) and Helicopsychidae (states 1 or 4). The development of the male maxillary palps also showed variation within one family and states 0, 1 or 2 were found in the Sericostomatidae, states 0 and 1 in both the Calocidae and Anomalopsychidae and states 1 and 2 in both the Conoesucidae and Helicopsychidae. In the cladistic analysis it was assumed that if the most primitive state of a character (e.g. the highest number of segments in the maxillary palps and the fullest complement of cells in the wings) occurs in genera of a particular family, it is the general state of that character for that family.

An analysis on this set of 59 characters using Hennig86 version 1.5 (Farris, 1988) determined shared characters in the twelve families without prior selection for any criteria. This produced two trees indicating parsimonious relatedness amongst the terminal taxa (Fig. 125). The Petrothrincidae, Barbarochthonidae and Hydrosalpingidae group closely together in both trees. These three families appear most closely related to the Helicophidae and Conoesucidae in the first tree and the whole cluster of families then shows close relationship to the Beraeidae. The second tree shows the three endemic South African families are apparently related to a cluster of families made up of the Beraeidae,

TABLE 1. The description of the status of 59 selected characters of larvae, pupae and adults from the eight presently described families of the Sericostomatoidea plus the three new families and the Antipodoeciidae. A status of 0 represents the primitive plesiomorphic state for a character. States such as 1,2 etc. represent derived apomorphies, usually but not always in a hierarchical phylogentic order. Where the primitive or derived state of a character could not be reasonably estimated valuation of character states commence with one.

	LARVAE
1.	Head; shape round 0, shape oval 1
2.	Head; without carina 0, with carina 1
3.	Antennae; near base of mandibles 0, midway between eyes and base of mandibles 1, close to eye 2
4.	Shape of ventral apotome; an equilateral triangle 1, an elongated triangle 2, quadrate or oval 3
5.	Ventral apotome; entirely separates genae 0, separates genae anteriorly only 1
6.	Pronotum; one single plate may be partially divided 1, one pair of large plates 2
7.	Pronotum; without a carina 0, with a carina 1
8.	Pronotum; with a posterior division 1, without a posterior division 2
9.	Pre-episternum; large and prominent 1, small and inconspicuous 2
10.	Pre-episternum; with upturned pointed apex 1, with blunt apex 2
11.	Mesonotum; a single plate 0, a pair of plates 1, more than two plates or sclerites 2
12.	Metanotum; one pair of small plates 1, membranous with setae 2, with more than two plates 3
13.	Forelegs; long and slender 0, short and stout 1
14.	Foreleg tarsal claw; shorter than tarsus 0, approximately as long as tarsus 1, longer than tarsus 2
15.	Midlegs; long and slender 0, short and stout 1
16.	Midleg tarsal claw; shorter than tarsus 0, approximately as long as tarsus 1
17.	Hindlegs; long 0, short 1
18.	Hindleg tarsal claw; shorter than tarsus 0, approximately as long as tarsus 1
19.	Abdomen with; small dorsal hump 0, large dorsal hump 1, lateral humps only 2
20.	Lateral abdominal humps with; setose sclerites 1, no sclerites or setae 2
21.	Ninth abdominal segment; with sclerite 1, with no sclerite 2
22.	Abdomen with; simple and branched gills 0, simple gills 1, no gills 2
23.	Eighth abdominal segment; with lateral tubercles 1, with no lateral tubercles 2
24.	Lateral abdominal fringe of setae; present 1, absent 2
25.	Anal prolegs; forming an apparent 10th segment 1, separated 2
26.	Anal claw with; 2-3 dorsal hooks 1, a dorsal comb 2
27.	Larval case; tubular and tusk shaped 0, limpet or shell shaped 1
28.	Larval case constructed of; pure silk 0, silk with some embeded sand grains 1, fine sand grains 2, a mixture of sand and plant matter 3, coralline or other algae 4
	PUPAE
29.	Antennae in male; shorter than body 0, as long as body 1, longer than body 2
30.	Antennae in female; shorter than body 0, as long as body 1, longer than body 2
31.	Inner margin of mandibles; feebly serrate 1, dentate 2
32.	Wing sheaths reach end of abdominal segment; five 1, six 2, seven 3, eight 4,
33.	No swimming fringes on tarsi 0, mid tarsi only fringed 1, fore and mid tarsi fringed 2
34.	Presegmental plates on abdominal segments; two to six 1, three to six 2, no plates present
35.	Post segmental plates on abdominal segment five with; one or two hooks 1, three hooks 2, two to four hooks 3
36.	Lateral fringe of abdominal setae on segments; six to eight 1, seven and eight 2, no lateral fringe of setae 3
37.	Pupal case anchored; around margin of case 1, by one or more anterior holdfasts 2

Table 1 continued on page 349

Table 1 continued from page 348

ADULTS	
38.	Antennae; shorter than length of forewing 0, same length as forewing 1, longer than length of forewing 2
39.	Maxillary palps in male; five segmented 0, three segmented 1, one or two segmented 2
40.	Ocelli; present 0, absent 1
41.	Facial warts; one pair at antennal bases 1, two pairs at antennal bases 2, one pair and median patch of setae at antennal bases 3
42.	Pronotum with; two pairs of warts 0, one pair of warts 1, single large wart (fused) 2
43.	Mesonotum with; one pair of warts 1, median field of setae 2, two lateral strips of setae 3, one or two setae only 4
44.	Mesoscutellum with; one pair of warts 0, a single large wart 1
45.	Leg spines; colourless 1, some black 2
46.	Thyridial cell in forewing; present 0, absent 1
47.	Androconia; absent 0, present on head 1, present on forewing 2, present on hindwing 3, present on fore and hindwing 4
48.	Discoidal cell in forewing; closed 0, open 1, absent 2
49.	Median cell in forewing; open 1, absent 2
50.	Sc and R1 in forewing; separate 0, joined 1
51.	In male forewing presence of forks: one to five 0; one, two, three and five 1; one and two 2; two and five 3; one, three and five 4; two or two and four 5; one, two and three 6; one and three 7
52.	In female forewing presence of forks: one, two, three and four, or one, two and five 1; one, two, three and five 2; one, two and three 3; one and two 4; two and five 5; two, four and five 6; one and three 7
53.	Jugal lobes in hindwing; large 0, small 1, absent 2
54.	In male hindwing presence of forks: one, two and five 1; two and five 2; one and two 3; one 4; two 5; five 6; none 7
55.	Wings; with no apparent coupling device 0, coupled by macrotrichia 1, coupled by hamuli 2
56.	Parameres on male genitalia; absent 0, present 1
57.	Male pre-anal appendages; with basal branch 1, unbranched 2, absent 3
58.	Female genitalia with vagina; sclerotised 1, not sclerotised 2
59.	Ninth abdominal sternite; separate from tenth 0; fused to tenth 1

Helicophidae and Conoesucidae. In both trees this grouping of families appears closest to the Antipodoeciidae.

It appears that certain synapomorphies link the three South African families (Table 2 characters 14, 29, 51 and 53).

Unfortunately the pupae of Antipodoeciidae are at present unknown which results in many missing characters being introduced into the analysis leading to a lack of resolution (Platnick, Griswold and Coddington, 1991). To overcome this problem all the pupal characters and a number of other characters for which character states in several of the families were missing were excluded and a cladistic analysis on only 44 characters was carried out (Fig. 126).

The most parsimonious single tree produced (Fig. 126) indicates a set of relationships rather different from that in Fig. 125. The Hydrosalpingidae are most closely related to the Helicophidae and these two families are then most closely related to the Conoesucidae. This cluster of families is related to the Chathamiidae and Calocidae. The family Petrothrincidae is closely related to the Barbarochthonidae which, however, appears most closely related to the Beraeidae which in turn are most closely related to the Antipodoeciidae. This cluster of families is most closely related to the Helicopsychidae and Sericostomatidae.

This second analysis is interesting because the Helicophidae are found in both Australasia and the Neotropical Region. It suggests that the Hydrosalpingidae are more closely related to the Australasian and South American families than to the other two South African families. This would strengthen the hypothesis of a temperate Gondwanaland ancestral origin of these families. A more

mhennig length 239 ci 42 ri 35 trees 2

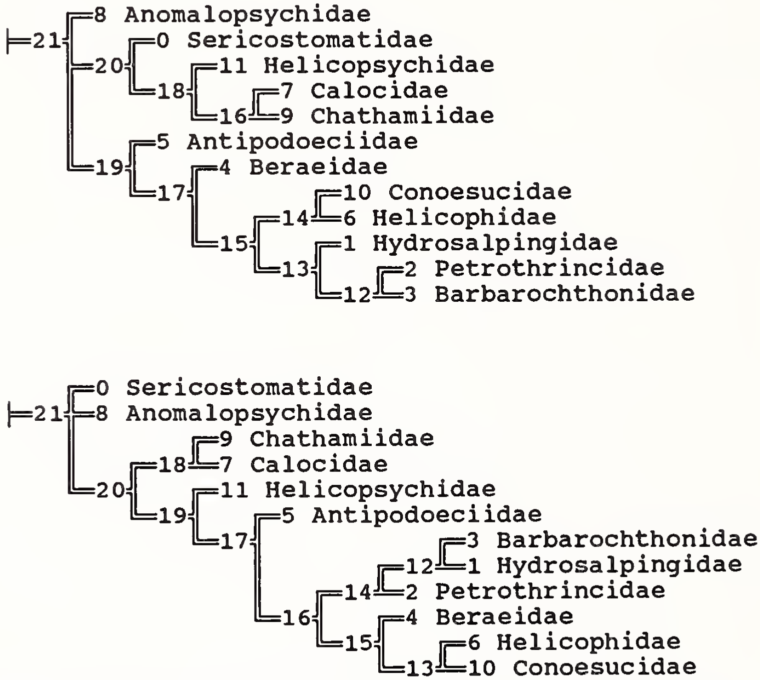


Fig. 125. Cladograms showing two possible relationships of the presently considered twelve families of Sericostomatoidea. Analysis based on 59 selected characters (Table 2).

mhennig length 188 ci 41 ri 37 trees 1

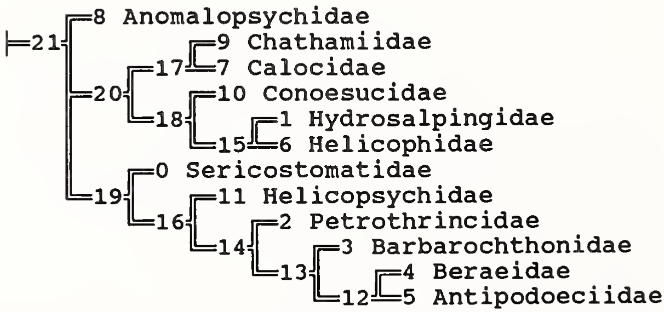


Fig. 126. Cladogram showing the possible relationships of the presently considered twelve families of Sericostomatoidea. Analysis based on 44 selected characters. Character states 18, 20, 29-37, 41 45, 58 and 59 (Table 2) were left out for this analysis.

TABLE 2. The status of 59 selected characters in the larvae, pupae and adults of the eight presently described families of the Sericostomatoidea plus the three new families and the Antipodoeciidae. Where there are variations for a character state within one family the most plesiomorphic state for that character in the family is chosen. (See Table 1 for explanation of character states). Abbreviations in the table refer to: Serico = Sericostomatidae, Hydro = Hydrosalpingidae, Petro = Petrothrincidae, Barba = Barbarochthonidae, Berae = Beraeidae, Antip = Antipodoeciidae, Helico = Helicophidae, Caloc = Calocidae, Anoma = Anomalopsychidae, Chat = Chathamiidae, Cono = Conoesucidae, Heli = Helicopsychidae. .S:6

Characters	Serico	Hydro	Petro	Barba	Berae	Antip	Helico	Caloc	Anoma	Chat	Cono	Heli
LARVAE												
1 Head shape	1	1	0	0	0	0	1	0	0	1	0	1
2 Head carina	1	0	0	1	1	0	1	0	1	0	1	1
3 Antenna pos	1	0	0	0	1	1	1	2	-	1	1	1
4 Vent apo shp	2	1	3	3	3	1	2	1	1	-	3	1
5 Genae sep	1	1	0	0	0	0	0	1	0	-	0	1
6 Pronot pls	1	1	1	1	1	1	1	1	1	1	1	1
7 Pron carina	0	0	0	1	1	1	0	0	1	0	0	0
8 Pron div	1	2	2	1	1	1	2	2	-	2	2	2
9 Pre epi size	1	2	1	1	1	-	2	2	2	2	1	2
10 Pre epi shp	1	1	1	2	2	-	1	1	1	1	2	1
11 Meso plates	1	1	1	1	0	1	2	1	0	1	1	1
12 Meta plates	3	1	2	2	2	2	3	2	1	3	3	3
13 Foreleg size	1	1	1	1	1	1	1	1	1	1	1	1
14 Claw size	1	1	1	1	1	-	2	1	0	2	2	0
15 Midleg size	0	0	1	0	0	1	1	0	0	0	1	0
16 Claw size	1	1	0	1	1	-	1	0	0	0	0	3
17 Hindleg size	0	0	0	0	0	1	1	0	0	0	0	0
18 Claw size	0	0	0	1	0	-	1	0	0	0	0	0
19 Abd hmps	2	0	1	1	0	-	0	0	2	1	0	2
20 Setal scler	1	1	2	1	2	-	2	-	2	2	2	-
21 9th abd scler	2	1	2	2	2	-	2	2	1	1	1	2
22 Abdom gills	1	2	0	2	0	2	2	2	2	0	0	1
23 Lat tuberc 8	1	1	2	2	1	1	1	1	2	1	1	2
24 Lat frnge seta	2	2	2	2	1	2	2	2	2	2	2	2
25 10 abd proleg	1	1	2	1	1	1	1	1	1	1	1	1
26 Anal claws	1	1	2	2	1	1	1	1	2	1	1	2
27 Case shape	0	0	1	0	0	0	0	0	0	0	0	1
28 Case struct	2	0	2	1	2	2	3	3	2	4	1	2
PUPAE												
29 M pup antenna	1	2	2	2	1	-	0	0	1	0	1	0
30 F pup antenna	1	2	0	1	0	-	0	0	1	0	1	0
31 Pup mandibles	1	2	1	1	1	-	2	1	2	1	1	1
32 Wing sheaths	2	2	3	4	1	-	-	-	4	-	-	-
33 Leg fringes	2	1	2	1	0	-	1	-	0	2	1	2
34 Preseg plates	2	1	2	1	3	-	2	2	2	2	2	2
35 Postseg pls	3	2	1	3	0	-	3	1	3	2	3	2
36 Ab setal fnge	3	2	3	2	3	-	1	2	3	3	1	3
37 Pup case anch	2	2	1	2	2	-	2	2	2	2	2	1
ADULTS												
38 Anten length	0	2	2	1	1	1	2	1	0	0	0	-
39 M maxil palps	0	0	0	1	0	1	0	0	0	0	1	1
40 Ocelli	1	1	1	1	1	1	1	1	0	1	1	1
41 Facial warts	1	1	3	2	-	-	1	-	1	-	-	-
42 Pronot warts	1	1	0	2	1	1	1	0	0	1	1	1
43 Mesonotal wts	1	4	2	2	1	1	4	3	1	3	4	2
44 Mesoscutel wts	1	2	1	2	2	2	1	1	2	2	1	1
45 Leg spines col	2	2	1	1	2	2	-	-	2	-	-	-
46 Thyrid cell	0	0	0	0	1	0	1	0	0	0	0	0
47 Androconia	1	0	0	3	2	0	0	2	0	2	0	0
48 Discoid cell	0	0	0	0	2	1	-	0	0	0	0	0
49 Median cell	1	1	1	1	2	2	2	2	2	2	-	1
50 Sc R1 joined	0	0	0	0	0	0	0	0	0	0	0	0
51 M Forks FW	1	6	6	6	5	6	3	1	1	2	1	7

52 F Forks FW	1	2	3	3	6	4	5	2	2	-	2	7
53 Wing lobes	0	0	0	0	2	1	1	0	2	1	1	1
54 M Forks HW	1	5	5	3	5	2	6	1	1	-	5	1
55 Wing coupling	1	1	1	1	1	0	3	1	0	1	1	3
56 Parameres	1	0	1	0	1	-	0	-	0	0	1	1
57 M prean app	2	1	2	1	2	3	2	2	2	1	2	2
58 Vagina scler	1	1	1	-	-	1	1	-	1	1	1	1
59 9 stern fused	0	1	1	1	1	1	0	-	1	-	-	-

careful determination of the relationships of the pupae would provide a clearer picture of the placement of the Antipodoeciidae.

The variation of possible character states within certain families of the Sericostomatoidea indicates either a polyphyletic origin for these families or else a convergence of character states. It confirms Wiggins' (1982) findings, that the relationships within the sericostomatoid families have not been sufficiently synthesised and fully resolved. A more detailed analysis of character states within world genera would possibly improve the determination of relationships within this interesting and diverse array of families which are so well represented in the southern hemisphere. More detailed morphological information on larvae, pupae and adults as well as behavioural and life history information are required before a comprehensive analysis of phylogenetic relationships within the Sericostomatoidea can be undertaken. A more rigorous analysis to test character consistency among all genera of the sericostomatoids is necessary before unbiased hypothesis testing of the monophyletic origin of the sericostomatoid family grouping can be performed.

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Dicrotendipes pilosimanus Kieffer: a description of all life stages, and features which distinguish it from *Dicrotendipes septemmaculatus* (Becker) (Insecta, Diptera: Chironomidae)

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ABSTRACT

Dicrotendipes pilosimanus Kieffer and *D. septemmaculatus* (Becker), both widespread in Africa and the Palaearctic, have been synonymized under *septemmaculatus* by some authors. This paper shows clearly that they are in fact both good species and can be separated in all life stages.

INTRODUCTION

Kieffer (1914) described *Dicrotendipes pilosimanus*, without illustrations, from a male and a female collected near Cape Town, South Africa. He described the wing markings, the hypopygium and the bearded tarsomeres of the male forelegs, the main distinguishing features of this species.

Freeman (1957) gave a fuller description of the male and a short description of the female *D. pilosimanus*. He also reduced the status of *quatuordecimpunctatus* Goetghebuer to a subspecies of *pilosimanus*. *D. quatuordecimpunctatus* is found in central and east Africa and is 'very similar to the typical subspecies in colour and general structure including hypopygium but differing in the absence of the tarsal beard'. With the limited data he had available, he considered that *pilosimanus* and *quatuordecinpunctatus* were the South African and east and central African representatives of one species.

His opinion was strengthened by the finding near Johannesburg, Transvaal (reported in Harrison, Keller and Dimovic, 1960; collected by Harrison) of what he regarded as apparent intermediate stages. However, the specimens mentioned in the paper were obtained from a small, swampy lake, Olifantsvlei, which was polluted by acid sulphates from the gold mines, and were not intermediates but were stunted specimens of *pilosimanus* from a very unsuitable, acid habitat.

These Olifantsvlei specimens have resulted in some taxonomic confusion and were one of the factors that led Epler (1988) to synonymize *pilosimanus* Kieffer with *septemmaculatus* (Becker) and *quatuordecimpunctatus* Goetghebuer. Cranston and Armitage (1988) also synonymized *pilosimanus* and *septemmaculatus*.

D. septemmaculatus is a widespread species found mostly in the Palaearctic, with the type locality, Tenerife, Canary Islands; Epler (1988) considers *quatuordecimpunctatus* to be a synonym but Contreras-Lichtenburg (1986, 1988) considers that these names apply to two distinct species, basing her opinion on larval and pupal characters. The present author has identified specimens found in and around Ethiopian Rift Valley lakes as *septemmaculatus*, as the larvae are similar to those described by Contreras-Lichtenberg (1988) for this species.

The aim of this paper is to define clearly in detail all stages of *pilosimanus*, using specimens collected near Cape Town, as well as some from Ethiopia and Zimbabwe, and to show that this species can be distinguished easily from *septemmaculatus*, using specimens from Ethiopia and the published descriptions.

METHODS

Adults were caught by sweeping vegetation near lakeshores; many were caught at lights. Some Ethiopian specimens were bred out in the laboratory in Addis Ababa and some South African specimens in the author's home near Cape Town. Larvae and pupae were caught by hand net in rivers and lakes.

All specimens were preserved in 70% alcohol and mounted in Canada Balsam dissolved in Cellosolve, or in Euparal. Specimens were not macerated in 10% KOH, as this may damage fine structures and may upset the arrangement of spermathecal capsules and ducts in females. Canada Balsam is the better mountant, as muscles are more transparent in it.

Measurements were made with an eyepiece micrometer and all drawings with a drawing tube on the microscope.

Generic definitions of males follow Epler (1988) and Cranston *et al*. (1989); of females Epler (1988) and Saether (1977); of pupae Pinder and Reiss (1986); and of larvae Pinder and Reiss (1983).

Morphological terminology is from Saether (1980).

Abbreviations used in this paper are:

AR = antennal ratio. Ratio of length of apical flagellomere to combined length of basal flagellomeres.

LR = leg ratio. Ratio of length of tarsomere 1 to length of tibia.

SV = 'Schenkel-Schiener-Verhältnis.' Ratio of femur plus tibia to tarsomere 1.

BV = 'Beinverhältnisse.' Combined length of femur, tibia and tarsomere 1 divided by combined length of tarsomeres 2 to 5.

DESCRIPTIONS

Dicrotendipes pilosimanus Kieffer 1914

Chironomus (Dicrotendipes) pilosimanus, Freeman 1957.
Dicrotendipes pilosimanus, Freeman and Cranston, 1980.
Dicrotendipes pilosimanus, Contreras-Lichtenberg 1986.
Dicrotendipes septemmaculatus (part), Epler 1988.

The type series of this species in the South African Museum, Cape Town consists of two specimens glued to a card on a pin; the male cotype has wings, with characteristic pattern of spots but the abdomen and forelegs are missing; the female cotype also has no abdomen but the wings are entire. The specimens were collected in the vicinity of Cape Town by Dr L. Péringuey.

The following descriptions are based on fresh material collected by the present author in the vicinity of Cape Town, and in the Ethiopian Highlands. All stages have been associated by rearing larvae.

Adult male (N = 14 mounted)

Close to generic definition in Cranston et al. (1989).

Wing length. 2.2 - 3.3 mm; mean 2.7 mm.

Colour (in alcohol). Head creamy yellow, antennae brown, mouthparts light brown. Thorax

background creamy yellow, mesonotal stripes brown with darker edges, central stripes fused, postnotum dark brown, median anepisternum II, epimeron II and preepisternum dark brown. Legs: all coxae creamy yellow; foreleg - femur light with dark ring at tip, knees light, tibia and tarsomeres 1 and 2 light with dark tips, tarsomere 3 light at base, darkening to tip, tarsomeres 4 and 5 dark; mid and hindlegs - femora light, tibiae light, darkened at tip (specially hind), tarsomeres 1 to 3 light, darkened at tip, 4 and 5 dark. Wings: light elongated spot at tip of r_{4+5}, dark spots - one central in r_{4+5}, one at base of r_{4+5} near cross vein continuing into m, one in m_{1+2}, one in m_{3+4}, 2 in anal cell (see Freeman's photograph). Abdomen background light, large darker spots in centre of tergites I - VIII, and lateral edges of tergites darkened, tergite IX and hypopygium darker.

Head. AR 2.3 - 3.1; mean 2.6. Frontal tubercles about twice as long as wide. Palp segments: small specimen, 31, 47, 146, 149, 205 µm; large specimen, 58, 62, 183, 171, 233 µm; large Ethiopian specimen, 78, 78, 183, 189, 280 µm. Five to six subapical sensilla on segment 3.

Thorax. Scutal tubercle present. Setation: Lateral antepronotals absent, dorsocentrals 10-15 (mean = 12) uniserial, number not obviously related to size, posterior prealars seven, scutellars seven to eight uniserial.

Wings. Setation: Brachiolum two, R 20-22, R_1 15-19, R_{4+5} 17-19, squama in large specimens 22, small specimens 16.

Legs. LR fore 1.35-1.5, mid 0.5-0.6, hind 0.6; SV fore 1.5-1.6; BV fore 1.8-1.9. Sensilla chaetica on tarsomere 1: midleg 10-13, hindleg absent. Beard on tarsomeres 1, 2 and 3 of foreleg. Ratio of beard setal length to width of tarsomere: tarsomere 1 about 3.8, tarsomere 2 in South African specimens 5.5-6.5, in Ethiopian specimens about 5. Tibia and tarsomeres of hind legs also have very long setae.

Hypopygium (Figs 1 and 3). Bands on anal tergite usually short and indistinct but clearer in some specimens and meeting centrally to form central band (Fig.1); about 16 or 17 apical anal tergite setae; apex of anal tergite with lateral hyaline lobes that show best on pinned specimens (Freeman) but usually become tucked under the tergite in specimens preserved in alcohol (see Fig. 1 where they are not visible); anal point down-turned. Superior volsella long and curved with two terminal setae; inferior volsella bowed dorsoventrally, bifid usually with five apical and one subterminal spinose setae, dorsally (Fig. 1), some with only the five apical ones; the Ethiopian specimens are like this but one has also a small subterminal seta on one side. Gonostylus evenly curved. Apodemes as in Fig. 3, the phallapodemes are very long and cross one another, in some specimens they are moved nearer to the anal point; the tips are usually blunt.

ADULT FEMALE (N = 8 mounted)

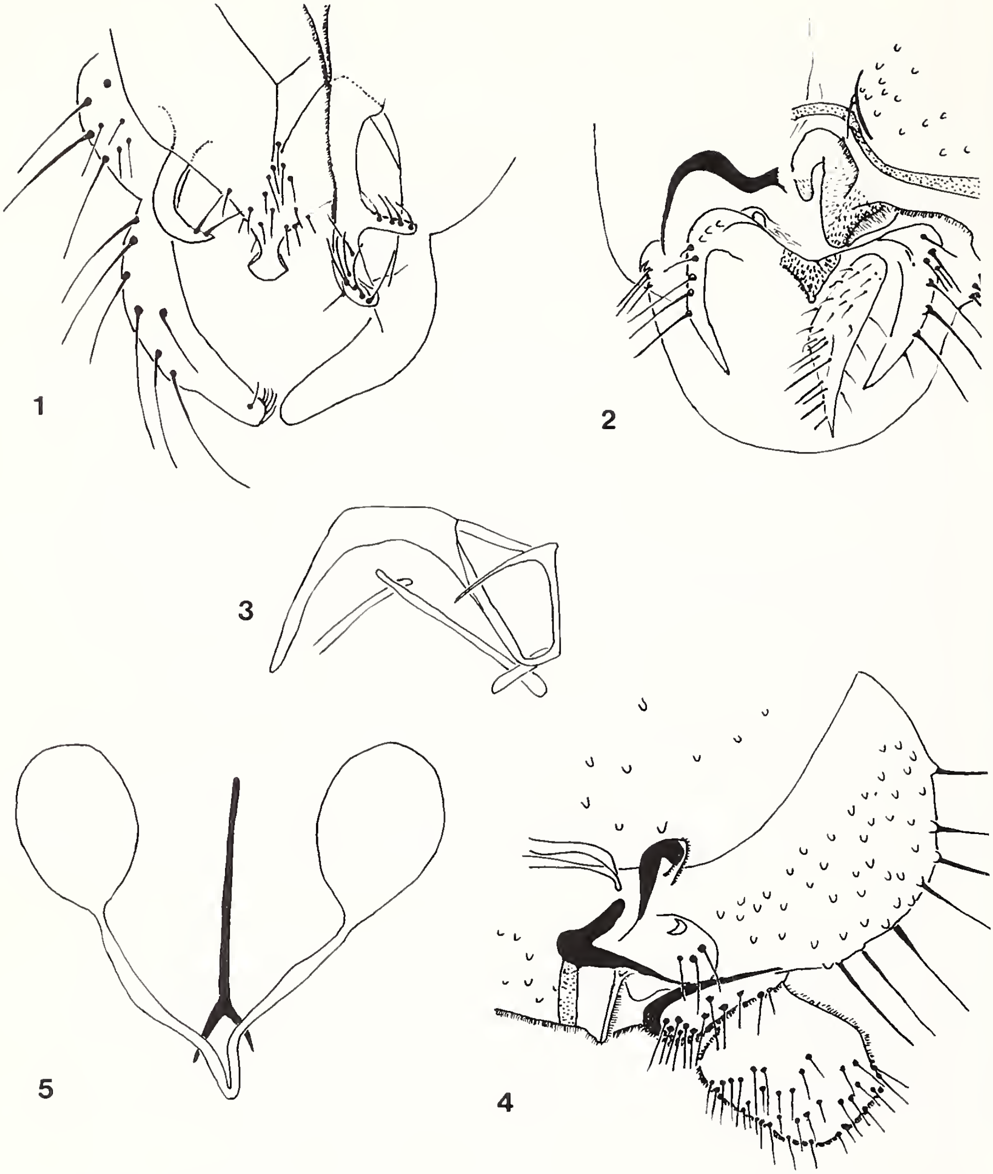
Close to generic definition.

Wing length. South African specimens 2.4 - 2.6 mm (mean 2.5 mm). Ethiopian specimens 3.1 - 3.6 mm (mean 3.3 mm).

Colour (in alcohol). Similar to male. Spots on abdominal tergites lighter than in male and edges of tergites only slightly darkened; tergite IX light. Genitalia: Sternite VIII brown and chitinized portions of IX and X brown.

Head. AR 0.45 - 0.50. Frontal tubercles similar to male. Palp segments in South African specimens: larger, 62, 47, 140, 140, 217 µm; smaller, 53, 53, 124, 142, 217 µm; in large Ethiopian specimen: 93, 78, 177, 186, 298 µm. Five to six subapical sensilla on segment 3.

Thorax. Scutal tubercle present. Setation: Lateral antepronotals absent, dorsocentrals 21-22, posterior prealars six to seven, scutellars 11-12 irregularly biserial.



Figs 1-5. *Dicrotendipes pilosimanus*. Adult: 1. male hypopygium; 2. female genitalia, ventral; 3. male phallapodemes; 4. female genitalia, lateral; 5. seminal capsules and ducts, dorsal.

Wings. Setation: Brachiolum 1-2, R 24-25, R_1 18-23, R_{4+5} 34-36, squama in South African specimens 20 - 25, in Ethiopian specimen about 30 partly biserial.

Legs. LR fore 1.48, mid 0.46 - 0.53, hind 0.59 - 0.62. Sensilla chaetica on tarsomere 1: midleg about 50 in South African specimens, about 94 in Ethiopian specimen, biserial to triserial; hindleg absent.

Genitalia (Figs 2, 4 and 5). Sternite VIII lightly chitinized, ventral ridge of VIII narrow; dorsomesal and ventrolateral lobes large, ventrolateral lobe is usually seen in side view (Fig. 2, right) but appears much larger when specimen is compressed; apodeme lobe small and narrow with microtrichia (Fig. 2, left); gonocoxapodemes light (stippled in figure), joined. Coxosternapodemes dark and curved (black in figures); gonocoxite IX small with three setae and small dorsal process (Figs 2 and 4). Segment X with chitinized anterior edge (Fig. 4) and with 8 - 13 setae per side (most specimens with 8), postgenital plate pointed. Labia without microtrichia. Seminal capsules (Fig. 5) with short, narrow neck, 127 - 158 µm long, ducts almost straight joining to common opening, tending to run parallel to each other a short distance before joining, central wider portion glandular.

PUPA (N = 25 mounted)

Similar to generic definition.

Colour. Exuviae are a fairly uniform yellowish brown, shagreen on abdomen darker.

Cephalothorax. Cephalic tubercles (Fig. 6) high, base granulose, frontal setae long; anterior of dorsum and humeral callus (see Epler, 1988) covered with short, blunt spines, rest of dorsum pebbled; dorsocentral setae 1 and 2 close together.

Abdomen (Fig. 7). Tergites I, and VI - VIII with weak reticulate pattern, not shown in figure. Tergite I bare, the rest with shagreen of posteriorly pointing spines, which become larger on posterior part of tergites II - VI, forming paired patches; on tergites V and VI these posterior spines are larger than on the other tergites, notably on VI. No shagreen in conjunctives. Posterior hook row on tergite II. No ventral spinal rows on sternites. Caudolateral spurs (Fig. 8) 1, 2 or 3 in the following pairs: 1 and 1 - 1 specimen; 1 and 2 - 10; 1 and 3 - 1; 2 and 2 - 6; 2 and 3 - 2; 3 and 3 - 5. Pedes spurii B are on segment II, and A on sternite IV.

LARVA (N = 16 mounted)

Similar to generic definition.

Colour. Head capsule light brown to brown, darker on 'cheeks', posterior rim black. Body green in life, yellowish preserved, anterior claws light brown, posterior claws brown.

Head capsule. Length 585 - 780 µm; mean 702 µm.

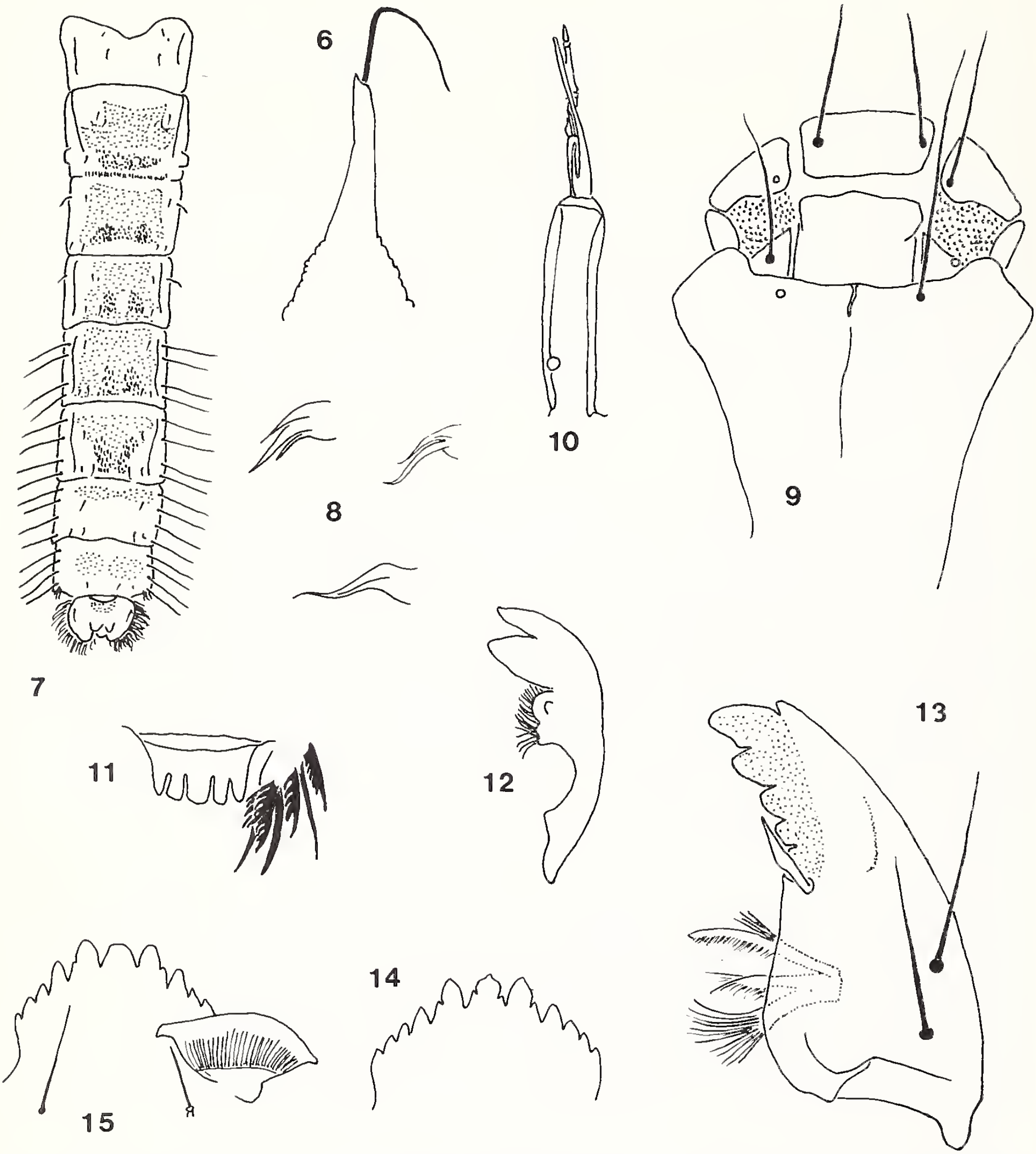
Dorsal surface of head (Fig. 9). Frontal apotome with small and narrow frontal process (Epler's term) or mark, frontal margin smooth, not crenate. Anterolateral projections short.

Antenna (Fig. 10). AR 0.63, blade slightly shorter than flagellum, segment 4 about six times as long as wide.

Labrum. S I with nine points. Pecten epipharynx (Fig. 11) with five teeth, chaetulae laterales comparatively small (Fig. 11), premandible with two teeth and brush (Fig. 12).

Mandible (Fig. 13). Dorsal tooth pale, four other teeth very dark. Pecten mandibularis (dorsal) with about 13 setae, mostly long and curved. Seta subdentalis pointed.

Mentum (Figs 14, 15). Unworn central tooth pointed with lateral notches, six lateral teeth, the



Figs 6-15. *Dicrotendipes pilosimanus.* Pupa: 6. cephalic tubercle; 7. abdomen, dorsal; 8. caudolateral spurs. Larva: 9. dorsal surface of head; 10. antenna; 11. pecten epipharynx; 12. premandible; 13. mandible; 14. mentum, unworn; 15. mentum, worn, and ventromental plate.

second forming a notch on the first. Most specimens were worn (Fig. 15). Ventromental plates have 40 - 46 strial ridges.

Maxilla (Fig. 16). Similar to Epler's figure showing generic structure. Numerous pointed chaetulae of palpiger on dorsal surface, not shown in Fig. 16.

Body. Claws of anterior parapod mostly long and curved, specially at tip, surface appears to be scaly at x1000 magnification, shorter claws pectinate towards tip, longer claws simple. Posterior claws simple; anal tubules short and blunt.

SPECIMENS EXAMINED. Adults: Numerous males and females netted on the shore of the small Noordhoek Lake, near Cape Town, ii.1992; 2 males and 2 females caught at lights, Addis Ababa, xi.1982; 2 males and 2 females caught at lights, Addis Ababa, ix.1983; 1 male and 1 female bred out from samples from stony run in polluted Kebena River, Addis Ababa, ix.1985; 1 male netted near sewage maturation ponds, Marendera (=Marendellas), Zimbabwe 18.x.61, Coll. A.D.H.. Pupae: 25 exuviae from Noordhoek Lake, ii.1992. Larvae: numerous larvae netted in weed beds in Noordhoek Lake, ii.1992; numerous larvae netted in stony runs in Kebena River, Addis Ababa, 1983-84.

COMMENTS. Kieffer's cotypes both have the wing markings characteristic of the species and the female has more than 20 squamal setae. Kieffer states that the male has long setae on tarsomeres 2-4 of the foreleg about five to six times as long as the thickness of the joints; this is similar to the specimens described here.

ECOLOGY. Harrison (1958) found this species in alkaline lakes in the Western Cape Province, South Africa, but not in those with a pH in the acid range. The specimens used in this paper came from weed beds of *Potomogeton* sp. in a small alkaline lake near Cape Town; *pilosimanus* is also found in slow-flowing alkaline to neutral streams in the same region.

In Zimbabwe it was breeding in the sewage maturation ponds at Marendera (=Marendellas), about 50 km from Harare.

In Ethiopia it was found in ponds, one above 4500 m in the Afro-alpine region of the Bale mountains, but none was found in the lakes; most larvae came from the torrential Kebena River (at about 2600 m) running through Addis Ababa. This stream received considerable amounts of organic pollution from the city, which encouraged this species as well as *Chironomus alluaudi* (Tesfaye Berhe *et al.*, 1989).

D. pilosimanus prefers slow-flowing streams and small eutrophic lakes and ponds. It is able to take advantage of polluted torrential streams in the same manner as *Chironomus* spp.

DISTRIBUTION. Found over most of southern Africa (Freeman, 1957); it is replaced over most of central and east Africa by *D. quatuordecimpunctatus* but occurs again in the Ethiopian Highlands; Contreras-Lichtenberg (1986) reports it from north Africa and Israel and the Balkans, as well as from the Oriental and Australasian regions.

Dicrotendipes septemmaculatus (Becker 1908)

Chironomus septemmaculatus Becker, 1908.
Dicrotendipes pilosimanus subsp. *quatuordecimpunctatus* (part?) Freeman 1957.
Dicrotendipes septemmaculatus, Cranston and Armitage 1988.
Dicrotendipes septemmaculatus, Epler 1988.

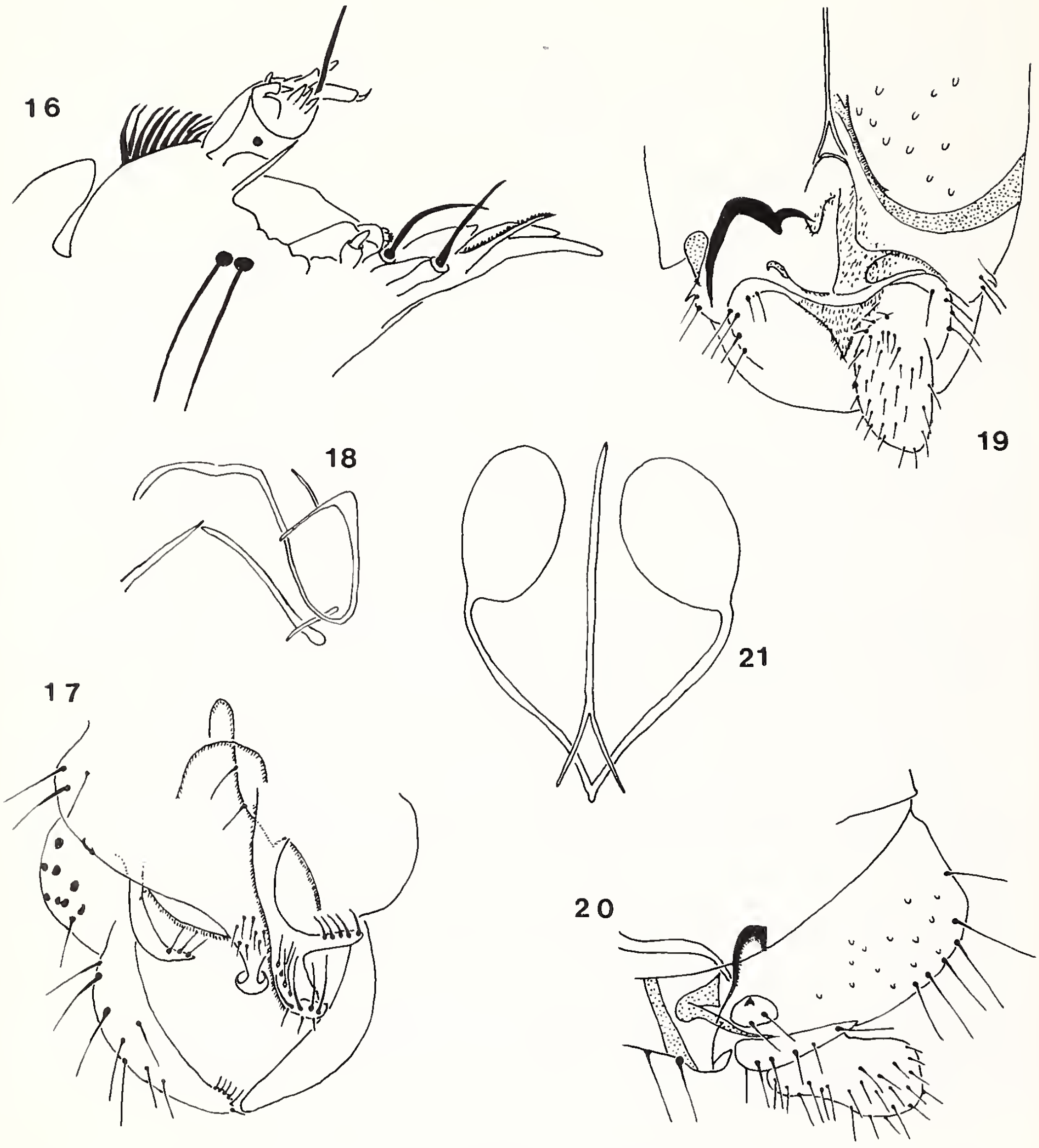


Fig. 16. *Dicrotendipes pilosimanus*. Larva: maxilla. Figs 17-21. *Dicrotendipes septemmaculatus*. Adult: 17. male hypopygium; 18. phallapodemes; 19. female genitalia, ventral; 20. female genitalia, lateral; 21. seminal capsules and ducts, ventral.

Dicrotendipes septemmaculatus, Contreras-Lichtenberg 1988.

Becker's description is based on one female type from the Canary Islands (Cranston and Armitage). Freeman does not illustrate the male of *quatuordecimpunctatus* but says that it is similar to that of *pilosimanus* s.str. except that it lacks the beard on the tarsomeres of the foreleg. Epler and Contreras-Lichtenberg describe the immatures.

Epler considers that *septemmaculatus* and *quatuordecimpunctatus* are conspecific but Contreras-Lichtenberg considers that they are distinct species; she separates them mainly on the structure of the dorsal sclerites of the larval head capsule. The larvae of the Ethiopian populations dealt with here are similar in some respects to her *septemmaculatus.*

Because of the controversy regarding the identity of *septemmaculatus, quatuordecimpunctatus* and *pilosimanus,* these Ethiopian specimens, including the female, are described here in detail.

ADULT MALE (N = 5 mounted)

Close to generic definition.

Wing length. 2.15 - 2.60 mm., mean 2.40 mm.

Colour. Unmounted specimens had been in alcohol for more than seven years by the time they were examined and had lost almost all their colour. Nevertheless, judging from other Ethiopian specimens mounted while they were still fresh, the colour pattern is very similar to that of *pilosimanus*, including the legs.

Head. AR 3.1. Frontal tubercles twice as long as wide. Palp segments: 71, 78, 177, 174, 267 µm. Five subapical sensilla on segment 3.

Thorax. Scutal tubercle present. Setation: Lateral antepronotals absent, dorsocentrals nine uniserial, posterior prealars five, scutellars six uniserial.

Wings. Dark markings as in Cranston and Armitage (1988), but elongated spot at tip of cell r_5 faint. Setation: Brachiolum 1, R 19 - 23, R_1 15-18, R_{4+5} 16 - 20, number does not seem to be correlated to size of wing, squama 10.

Legs. LR fore 1.5, mid 0.5, hind 0.6; SV fore 1.4-1.5; BV fore 1.8. Colour: foreleg with dark tips to femur, tibia and tarsomeres 1 and 2, rest of tarsomeres wholly dark; midleg with femur plain, dark tips to tibia and tarsomeres 1-4, 5 dark; hindleg with femur plain, dark tips to tibia and tarsomeres 1-3, 4 and 5 dark. Sensilla chaetica on tarsomere 1: midleg 10, hindleg absent.

Hypopygium (Figs 17, 18). Bands on anal tergite short and indistinct (not in figure), median anal tergite setae absent, about 10 apical anal tergite setae; apex of anal tergite with lateral hyaline lobes; anal point down-turned. Superior volsella long and curved with two to three terminal spinose setae (Table 1); inferior volsella bowed dorsoventrally, bifid, with strong apical spinose setae, the variable number of which appears to be related to size of specimen (Table 1). Gonostylus evenly curved. Apodemes as in Fig. 18.

ADULT FEMALE (N = 5 mounted)

Close to generic definition.

Colour. Similar to female *pilosimanus,* including the legs.

Wing length. 2.3 mm.

Head. AR 0.4. Frontal tubercles similar to male. Palp segments: 47, 47, 99, 124, 189 µm. About six subapical sensilla on segment 3.

TABLE 1. *Dicrotendipes septemmaculatus.* Number of terminal spinose setae on volsella related to wing length. (Left/right)

Wing length mm	2.60	2.40	2.35	2.15
Sup. volsella	3/3	2/2	2/3	2/2
Inf. volsella:				
main	7/8	7/7	5/6	5/5
branch	4/4	5/5	4/4	3/3

Thorax. Scutal tubercle present. Setation: Lateral antepronotals absent, dorsocentrals 16 uniserial, posterior prealars five, scutellars four or five.

Wings. Markings as in male. Setation: Brachiolum two, R 26, R_1 20, R_{4+5} 35, squama six.

Legs. LR fore 1.5, mid 0.5, hind 0.6. Markings as in male. Sensilla chaetica on tarsomere 1: midleg 34 - 46 partly biserial; on hindleg absent or one. Three of the specimens had one on tarsomere 2 of midleg.

Genitalia (Figs 19, 20 and 21). Sternite VIII lightly chitinized; ventral ridge of VIII narrow; dorsomesal and ventrolateral lobes large (Fig. 19, right), apodeme lobe small and narrow, with microtrichia (Fig. 19, left); gonocoxapodemes light, do not appear to be joined. Coxosternapodemes dark and curved; gonocoxite IX small with two setae and small, dorsal chitinized process. Segment X with six setae per side, postgenital plate pointed. Labia without microtrichia. Seminal capsules (Fig. 21) oval with short neck, 108 µm long, ducts almost straight joining at an angle of about 45o or more to common opening, central part glandular.

PUPA

None found, but pupae are described by Contreras-Lichtenberg and Epler.

LARVA (N = 7 mounted)

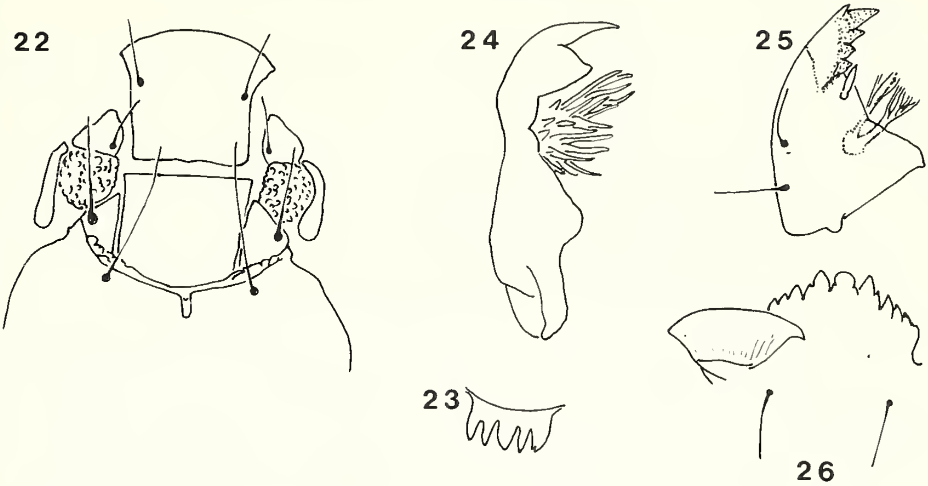
Similar to generic definition. Drawings were made from a newly moulted 4th instar with mouthparts unworn.

Head capsule. 520 - 585 µm long; mean 553 µm.

Dorsal surface of head (Fig. 22). Frontal apotome with distinct frontal process or mark, frontal margin crenate on either side of this. Anterolateral projections small and short.

Antenna. Very similar to those of *D. pilosimanus.* AR 0.73. Antennal blade longer than flagellum, segment 4 about six times as long as wide.

Labrum. Similar to *pilosimanus.* S I with nine points. Pecten epipharynx (Fig. 23) with five, six or seven teeth. Premandible (Fig. 24) with two teeth and brush.



Figs 22-26. *Dicrotendipes septemmaculatus.* Larva: 22. dorsal surface of head; 23. pecten epipharynx; 24. premandible; 25. mandible; 26. mentum and ventromental plate.

Mandible (Fig. 25). Dorsal tooth pale, the four other teeth very dark, seta subdentalis simple and pointed.

Mentum (Fig. 26). Central tooth rounded and notched, six lateral teeth, the second forming a notch on the first. The ventromental plates have 26 - 30 strial ridges.

Maxilla. Similar to that of *pilosimanus.*

Body. Claws of anterior parapods mostly long and thin, the larger with ends hooked and minutely serrate towards tip, the smaller not hooked or serrate. Claws of post parapods not serrate, anal tubules slightly tapered with rounded tips, much shorter than parapods.

SPECIMENS EXAMINED. Adults: numerous males and 5 females, caught at lights, Lake Awasa, Rift Valley, 15.iii.1981; 1 male and 1 female, netted at Lake Awasa, 25.viii.1984; Larvae: 4 netted in weed beds, Lake Awasa, 1983-84; 1 from shallow bottom, Lake Ziway, 5.vii.1984; 1 from Akaki River, downstream from Debre Zeit, 16.ii.1984; 1 from Bulbulla Shet flowing out of Lake Langano, Rift Valley, 24.ii.1984.

COMMENTS. The female holotype of *septemmaculatus* from the Canary Islands has been mounted and redescribed by Cranston and Armitage. The arrangement of the spermathecal ducts and the number of squamal setae (about 10) in the Canary Island specimen seem to indicate that the Ethiopian specimens are correctly placed in this species. Also the association here between the females, males and larvae indicates that the specimens described by Contreras-Lichtenberg and Epler also are correctly placed in this species.

In addition, Cranston and Armitage redescribed the male lectotype of *Stictochironomus sexonotatus* Goetghebuer, from southern Spain, and consider it to be a junior synonym of *D. septemmaculatus.* The number of terminal spinose setae on the superior volsella (three) and inferior

volsella (six) fit in with *septemmaculatus* and not *pilosimanus.* (See Table 2).

ECOLOGY. The larvae were found in weed beds, on the bottom of shallow lakes or in slow-flowing rivers.

DISTRIBUTION. Epler lists material from the Afrotropical Region, the southern Palaearctic, Australian, and Oriental Regions. In Africa this species or its (?) allied species *quatuordecimpunctatus,* has not yet been found south of Zimbabwe although one of them probably exists in the subtropical regions of South Africa.

TABLE 2. *Dicrotendipes pilosimanus* and *D. septemmaculatus* contrasted.

	D. pilosimanus	*D. septemmaculatus*
Adult male:		
wing length	2.20 - 3.30 mm	2.15 - 2.60 mm
dorsocentrals	10 - 15	9
squamal setae	16 - 22	about 10
beard on tarsomeres of foreleg	present, longest on 2 and 3	absent
hypopygium: terminal spinose setae on inferior volsella	5, in all specimens	5 - 8, depending on size
apical anal tergite setae	about 16-17	about 10
Adult female:		
dorsocentrals	21 -22	16
squamal setae	S. Africa: 20-25 Ethiopia: about 30	6
genitalia: seminal ducts	running almost parallel to each other just before joining	joining at an angle of about 45^{o} or more
Pupa:-		
cephalic tubercle	large	not specially large
shagreen on conjunctives	absent	IV/V, V/VI, VI/VII
caudolateral spurs of VIII	1, 2 or 3	one
Larva:		
head capsule length	585-780 mm.	520-585 mm.
frontal apotome	frontal margin smooth	frontal margin crenate
ventromental plates	40-46 strial ridges	26-30 strial ridges

DISCUSSION

The two species, *D. pilosimanus* and *D. septemmaculatus,* are very similar and obviously fall into the same species group. However, it is apparent from Table 2 that it is fairly easy to distinguish all life stages.

The males can be separated by means of the tarsal beard and large number of squamal setae of *pilosimanus,* and the females by the large number of squamal setae of *pilosimanus* and its special and consistent arrangement of the seminal ducts which run almost parallel to each other before joining.

The pupae can be separated by the multiple caudolateral spines of *pilosimanus.* Also, the shagreen on tergites II and V is more extensive than that of *septemmaculatus* and *quatuordecimpunctatus,* as illustrated by Contreras-Lichtenburg.

The larvae can be separated by the smooth frontal margin of their frontal apotome and the larger number of striae (40-46) on the ventromental plate of *pilosimanus.*

The two species differ also in their ecological requirements. *D. pilosimanus* is found in productive lakes and ponds, mainly in weed beds, but not where the pH is in the acid range (Harrison, 1958). It is also found in slow-flowing streams. In Ethiopia it was found in a torrental stream strongly polluted with organic matter from the city of Addis Ababa; here it formed part of the usual `pollution community' of *Tubifex, Chironomus,* Psychodidae and resistant Baetidae (Tesfaye Berhe *et al.,* 1989). It was also found in a pond in the Afro-alpine region of the Bale Mountains. In Zimbabwe it was found in sewage oxidation ponds but nowhere else, although the region had been extensively collected by the author during 1961-63 (Harrison: unpublished data); other small ponds and impoundments there contained *quatuordecimpunctatus.*

In Ethiopia *D. septemmaculatus* was found in Rift Valley lakes, mainly in weed beds but also on shallow bottoms (Tilahun Kibret and Harrison, 1988, listed as *quatuordecimpunctatus;* Tudorancea *et al.,* 1988, under *Dicrotendipes* spp.). It is yet to be found in South Africa. Dejoux (1983) does not report it from Lake Chad although he did have some unidentified *Dicrotendipes* larvae.

It is too early to attempt to resolve the *septemmaculatus* vs. *quatuordecimpunctatus* controversy. If they are separate species they resemble one another more closely than either resembles *pilosimanus.* More material of all life stages from the type localities is required, preferably correlated by rearing.

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